WILSON ORNITHOLOGICAL CLUB

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Devoted to Natural History, Primarily that of the Prairie States

Founded by J. A. Nieuwland, C.S.C.

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A Miocene Flora from Thorn Creek, Idaho

Helen V. Smith

The Thorn Creek locality is on the southern edge of the Boise (or Idaho) Basin. The fossiliferous strata were discovered by members of a Civilian Conservation Corps in the fall of 1937, and were exposed in a road-cut about one mile up from the mouth of the creek in Sec. 30, T. 5 N., R. 5 E. approximately ten miles south of Idaho City, Boise County, Idaho.

The plant impressions proved to be extremely well preserved. Collections were made for me in 1937 and 1938 by Orma J. Smith and H. M. Tucker of the College of Idaho. I made fairly large collections in 1937 and again in 1939. Between 1937 and August 1939 a large amount of material above the fossil bed was removed by a landslide leaving a broad exposure. In this new exposure we found only a few additional species, indicating that a representative collection had very likely been obtained.

I acknowledge with thanks the interest of Dean Orma J. Smith and Professor H. M. Tucker and the collections they made for me; and of Professor E. B. Mains who made available the collections of the University of Michigan Herbarium.

The most extensive general study of the Boise Basin is that of Lindgren (25). More recent work has been done by Jones (17) and Ballard (4). Lindgren collected plant fossils from five localities, one of which was in the basin and the others along Boise Ridge which divides the basin from the Payette River drainage. Knowlton (21) studied the plant impressions from Lindgren's collections and identified thirty-two species, seventeen of which he described as new. Lindgren (25) proposed the name Payette formation for the lacrustrine sediments of that area. In 1900 he (26) reported additional plant remains from this formation at Sucker Creek, a small stream on the west side of the Owyhee Mountains of Idaho about fifty miles southwest of the Thorn Creek locality. Lake beds mapped as belonging to the Payette formation occupy an area of about seven square miles near Idaho City. They occur on both sides of Moore Creek about a half mile below Warm Springs and ten miles north of Thorn Creek. They consist of partially consolidated white sand and clay. Fossil plants collected by Lindgren from these beds included the following: *Equisetum, Pinus* fruit, *Sequoia angustifolia?, Ulmus speciosa, Celastrus Lindgreni,* and *Trapa americana.*

With the exception of my preliminary report (34) on some of the Thorn Creek fossils, no further paleobotanical studies seem to have been made in the

Boise Basin-Boise Ridge region. A number of investigations have been made at Sucker Creek and in the vicinity of Weiser, Idaho. Chaney (13), Berry (7), Brooks (9), Arnold (1, 2, 3) and Smith (32, 33, 35) have studied the Sucker Creek flora. Fossils from the Weiser beds have been studied by Berry (8), Dorf (16) and Smith (31). As a result of these studies and Kirkham's work (18), the plant-bearing strata of southwestern Idaho and adjacent Oregon have been divided into two series, the (older) Payette and the (younger) Idaho formation. Kirkham (18) has presented evidence for a Miocene age for the Payette and transitional or early Pliocene age for the Idaho formation.

The Boise Basin is a roughly circular area lying in the south central part of the Central Province of the Rocky Mountain System. It constitutes the drainage area of Moore Creek and Grimes Creek and is about fifteen miles in diameter. The floor at Idaho City has an elevation of 4000 feet. The basin is sharply separated from the surrounding country by the high divides of the Boise Mountains and irregular spurs of the Sawtooth Range which attain elevations of nearly 8000 feet.

The geologic succession of events in the basin is not well established. According to Lindgren (25) erosion alone would not have produced the basin, but must have been accompanied by block faulting. He believed that the Miocene sediments of the basins of southwestern Idaho were deposited in a large lake, Lake Payette. Kirkham (18) who has done more recent work, does not envisage a single large lake as being responsible for all this deposition. He suggests that streams, fans, deltas and small temporary lakes may have played a part as depositing agencies.

It is probable that the climatic conditions at Thorn Creek are almost the same as those at Garden Valley and intermediate between those of Boise and McCall. The available data are summarized in Table 1.

The forest belts of the northern and central Rocky Mountains extend through three life zones: Transition, Canadian, and Hudsonian. The Boise Basin is almost wholly included in the Transition, but the higher ridges surrounding it extend into the Canadian zone. The vegetation in the lower Thorn Creek Valley is typical of the arid Transition.

In the northern Rocky Mountains of Montana and Idaho the principal forest trees are coniferous. The main stream border trees according to Kirkwood (20) are *Populus trichocarpa, Alnus tenuifolia* and *Betula fontinalis*. These three species occur along almost every stream on the western slope of the Continental Divide in the northern Rockies. *Populus tremuloides, Salix cordata, S. fluviatilis, Cornus stolonifera* and others may also occur. The principal forest trees are *Pinus ponderosa, P. contorta, P. albicaulis, Larix occidentalis, Pseudotsuga taxifolia, Picea Engelmanii, Abies lasiocarpa* and *Juniperus scopulorum*. Such species as *Pinus monticola, Tsuga heterophylla, Abies grandis* and *Thuja plicata* may be locally important. Plate 1 illustrates the present vegetation at Thorn Creek.

A collection was made of all woody species found between the first fork of

TABLE 1.—Weather data from southwestern Idaho localities near Thorn Creek.

Weather station	Boise	Garden Valley	Idaho City	McCall
Elevation	2,739	3,300	4,000	5,025
Life zone	Sonoran	Transition	Transition	Canadian
Average annual precipitation	13.38	21.79	21.31	25.56
Months with less than one inch precipitation	June-Sept.	June-Sept.	June-Sept.	July-Aug.
Months of maximum precipitation	Dec. Jan.	Nov. Jan.	Nov. Feb.	Dec. Jan.
Amount of maximum monthly precipitation in inches	1.67 1.90	3.49 3.42	3.04 3.07	3.64 3.59
Average annual snowfall in inches	24.5		93.7	134.8
Average temperature	51.2			39.5
Highest temperature	121			104
Lowest temperature	–28			–34
Average number of frostless days	169	107	88	76

Thorn Creek and its mouth. This collecting covered about five miles in the lower end of the valley and yielded the following species: *Acer glabrum* Torr., *Alnus tenuifolia* Nutt., *Amelanchier alnifolia* Nutt., *Artemesia cana* Pursh, *Betula fontinalis* Sarg., *Ceanothus velutinus* Dougl., *Cornus stolonifera* Michx., *Crataegus Douglasii* Lindl., *Holodiscus discolor* Maxim., *Lonicera involucrata* Banks, *Mahonia Aquifolium* Nutt., *Opulaster malvaceus* (Greene) Kuntze, *Philadelphus Lewisii* Pursh, *Pinus ponderosa* Laws., *Populus angustifolia* James, *P. tremuloides* Michx., *P. trichocarpa* T. & G., *Prunus demissa* (Nutt.) Walp., *Pseudotsuga taxifolia* (Poir.) Britt., *Purshia tridentata* (Pursh) DC., *Rhamnus Purshiana* DC., *Rhus Toxicodendron* L., *Ribes americanum* Mill., *R. cereum* Dougl., *Rosa acicularis* Lindl., *Rubus leucodermis* Dougl., *R. strigosus* Michx., *Salix exigua* Nutt., *S. Scouleriana* Barratt, *Sambucus glauca* Nutt., *Sorbus scopulina* Greene, *Spirea lucida* Dougl., and *Symphoricarpos racemosus* Michx.

Composition of the Fossil Flora

Polypodiaceae
- *Pteris calabazensis* Dorf.

Pinaceae
- *Pinus quinifolia* n. sp.
- *Pinus* sp. (seed)
- *Picea lahontensis* MacG.
- *Pseudotsuga Masoni* MacG.
- *Abies laticarpa* MacG.
- *Abies parviseminis* LaMotte
- *Abies* sp. (cone scale)
- *Sequoia affinis* Lesq.
- *Sequoia Langsdorfii* (Brongn.) Heer
- *Thuja Garmani* Lesq.

Typhaceae
- *Typha Lesquereuxi* Cockerell

Salicaceae
- *Populus balsamoides* Goepp.
- *Populus Booneana* n. sp.
- *Populus dolichophylla* n. sp.
- *Populus eotremuloides* Knowlt.
- *Populus washoensis* Brown
- *Salix boisiensis* n. sp.
- *Salix Schimperi* Lesq.
- *Salix spokanensis* (Berry) Brown
- *Salix venosiuscula* n. sp.

PLATE 1

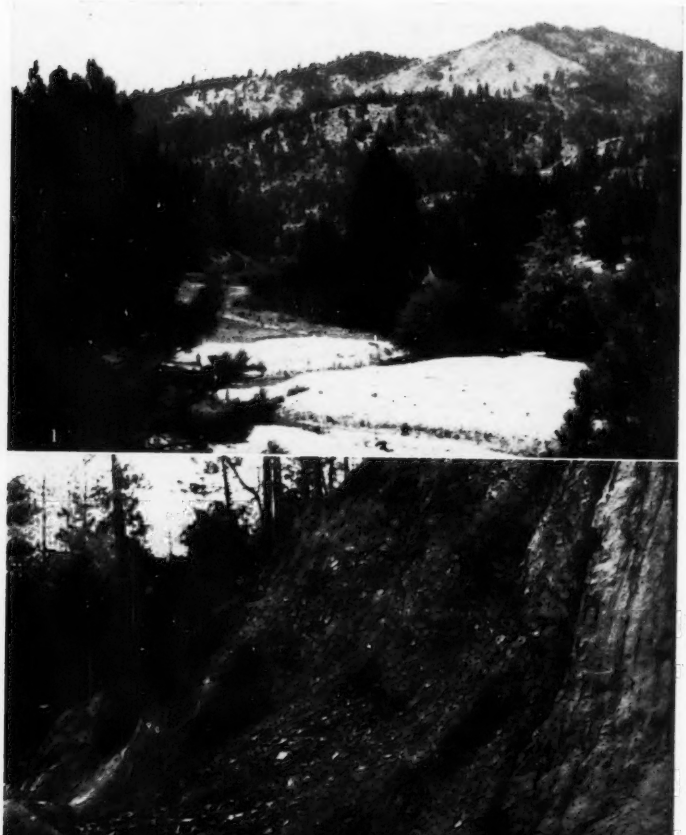

Fig. 1. A view of the lower Thorn Creek Valley showing the general topography and vegetation. The conifers on the hillsides are yellow pine and the typical deciduous association along the stream is composed of birches, alder and willows. Fig. 2. A view of the road-cut from which the fossils were obtained. The folding of the bed is evident.

Juglandaceae
Carya egregia (Lesq.) LaMotte
Carya pecanoides (Chaney) n. comb.
Betulaceae
Carpinus payettensis n. sp.
Betula idahoensis H. V. Smith.
Betula lacustris MacG.
Alnus carpinoides Lesq.
Alnus corallina Lesq.
Alnus sp. (cones)
Fagaceae
Fagus pacifica Chaney
Castanopsis angustifolia n. sp.
Quercus boisiensis n. sp.
Quercus Bretzi Chaney
Quercus Browni Brooks
Quercus clarnensis Trelease
Quercus deflexiloba n. sp.
Quercus Eoprinus H. V. Smith
Quercus Maccannii Berry
Quercus Merriami Knowlt.
Quercus payettensis Knowlt.
Quercus pseudolyrata Lesq.
Quercus simulata Knowlt.
Quercus Tuckeri n. sp.
Ulmaceae
Ulmus paucidentata H. V. Smith
Magnoliaceae
Magnolia oregoniana Chaney
Saxifragaceae
Ribes sp.
Rosaceae
Amelanchier dignata (Knowlt.) Brown
Amelanchier subserrata n. sp.
Crataegus microcarpifolia Arnold
Pyrus heteromorpha n. sp.
Cercocarpus cuneatus Dorf
Prunus Chaneyi Condit
Prunus covea Chaney
Meliaceae
Cedrela (?) *pteriformis* (Berry) Brown
Aceraceae
Acer glabroides Brown
Acer negundoides MacG.
Acer Osmonti Knowlt.
Acer Scottiae MacG.
Acer sp. (samara)
Acer sp. (samara)
Sapindaceae
Sapindus idahoensis n. sp.
Rhamnaceae
Rhamnus idahoensis Brown
Rhamnus sp.
Ceanothus sp.
Tiliaceae
Tilia parvulifolia n. sp.
Ericaceae
Arbutus idahoensis (Knowlt.) Brown
Arbutus Matthesii Chaney
Arbutus opaca n. sp.
Rhododendron idahoensis H. V. Smith
Ebenaceae
Diospyros elliptica Knowlt.
Oleaceae
Fraxinus leptocarya n. sp.
Caprifoliaceae
Symphoricarpos elegans (Lesq.) Smith

In order to show more clearly the numerical representation, Table 2 has been prepared. Only the well preserved impressions were retained and counted from the first year's collecting. During the collecting season of 1939 counts were made of all indentifiable specimens.

Relationships with Living Floras

The aspect of the Thorn Creek fossil flora is typically modern. The fossils have been carefully compared with living species and those to which they are most similar are taken to be the most closely related and presumably indicate the climatic conditions under which the fossils lived. Whether or not this assumption is justified cannot be discussed here further than to say that to the workers who are now most active, it appears to give the most reasonable approach to a difficult problem.

Studies of living species have been made both in the field and on herbarium specimens. In the University of Michigan Herbarium the species comprising the flora of the eastern United States and the Appalachian region are well represented. Field studies of this flora have been made in the vicinity of Ann Arbor, Mich., and in the Great Smoky Mountains of Tennessee and North Carolina. The flora of the Rocky Mountains was studied in south central

Idaho. Field work on the Pacific Coast floras was carried on in the Olympic Mountains of Washington and in northern California and southern Oregon.

TABLE 2.—List of named species and the number of specimens of each identified from the Thorn Creek flora.

Species	Number of Specimens	per cent	Species	Number of Specimens	per cent
Quercus Eoprinus	852	43	*Acer Osmonti*	3	
Fagus pacifica	348	17	*Arbutus Matthesii*	3	
Quercus pseudolyrata	142	7	*Betula idahoensis*	3	
Salix Schimperi	91	5	*Fraxinus leptocarya*	3	
Acer glabroides	86	4	*Picea lahontensis*	3	
Total of first five	1519	76	*Populus balsamoides*	3	
Populus eotremuloides	63	3.1	*Symphoricarpos elegans*	3	
Ulmus paucdentata	33	1.7	*Thuja Garmani*	3	
Quercus Merriami	31	1.6	*Abies laticarpus*	2	
Quercus clarnensis	27	1.3	*Alnus carpinoides*	2	
Populus dolichophylla	26	1.3	*Arbutus idahoensis*	2	
Total of second five	180	9	*Arbutus opaca*	2	
Quercus Bretzi	23		*Carya egregia*	2	
Quercus payettensis	22		*Crataegus microcarpifolia*	2	
Rhododendron idahoensis	22		*Prunus covea*	2	
Quercus simulata	20		*Pseudotsuga Masoni*	2	
Salix venosiuscula	19		*Quercus deflexiloba*	2	
Total of third five	105	5	*Salix boisiensis*	2	
Quercus Tuckeri	18		*Abies parviseminis*	1	
Castanopsis angustifolia	18		*Acer negundoides*	1	
Quercus Browni	17		*Amelanchier dignata*	1	
Sequoia affinis	17		*Amelanchier subserrata*	1	
Populus washoensis	16		*Carpinus payettensis*	1	
Total of fourth five	86	4	*Carya pecanoides*	1	
Pinus quinifolia	12		*Cedrela pteriformis*	1	
Sapindus idahoensis	7		*Cercocarpus cuneatus*	1	
Quercus boisiensis	6		*Diospyros elliptica*	1	
Salix spokanensis	6		*Magnolia oregoniana*	1	
Sequoia Langsdorfii	6		*Prunus Chaneyi*	1	
Alnus corrallina	5		*Pteris calabazensis*	1	
Populus Booneana	5		*Quercus Maccanni*	1	
Pyrus heteromorpha	5		*Rhamnus idahoensis*	1	
Acer Scottiae	4		*Tilia parvulifolia*	1	
Betula lacustris	4		*Typha Lesquereuxi*	1	
Total, last ten	60	3	Total, this column	60	
Total, this column	1950	97	per cent total		3
Total number of species included in this count				64	
Total number of specimens included in this count				2010	

These studies indicated that the Thorn Creek fossils may be divided into groups on the basis of the geographic range of similar living types, namely: (1) those whose nearest living equivalents grow in the Rocky Mountains, and more particularly in the northern Rockies, and (2) those now represented by living allies in the eastern United States, especially the Appalachian region. Of less importance are (3) the species now represented on the humid Pacific Coast and (4) those in the arid southwest.

Some of the living species such as *Pteris (Pteridium) aquilina* and *Salix cordata* are represented in all of these areas, and are, therefore, not important as indicators of floristic affiliations or of climatic conditions.

The absence of an eastern Asiatic element so common in many of the western Tertiary floras is of interest. Many of the genera which have become extinct in the West are found in eastern Asia as well as eastern United States, but in practically all cases I believe that the Thorn Creek fossils are more similar to the American species.

On the basis of the number of species, the northern Rocky Mountain and Appalachian elements are about equally important. The Rocky Mountain element includes woody species that occur in the north or at high elevations farther south. Many of these species correspond to those that comprise the major forest cover of the mountains, while others grow along the streams or in moist valleys.

The Rocky Mountain element is of particular interest and is here treated in two parts: first, those species whose living equivalents were collected at Thorn Creek, and second, those for which the living equivalents occur elsewhere in the region.

Of the twenty-eight living woody genera now present at Thorn Creek fourteen are represented in the fossil flora. All except *Pseudotsuga* are far ranging in North America. The genera which are represented by both living and fossil species at Thorn Creek are: *Acer, Alnus, Amelanchier, Betula, Ceanothus, Crataegus, Pinus, Populus, Prunus, Pseudotsuga, Rhamnus, Ribes, Salix* and *Symphoricarpos*.

A more detailed picture of the similarity between the floras is given by a parallel listing of the related living and fossil species found at Thorn Creek:

Fossil species	Similar living species
Acer glabroides	*A. glabrum*
Amelanchier dignata	*A. alnifolia*
Betula lacustris	*B. fontinalis*
Populus Booneana	*P. tremuloides*
Populus dolichophylla	*P. angustifolia*
Populus eotremuloides	*P. trichocarpa*
Pseudotsuga Masoni	*P. taxifolia*
Pteris calabazensis	*P. aquilina*
Rhamnus idahoensis	*R. Purshiana*
Salix boisiensis	*S. Scouleriana*
Symphoricarpos elegans	*S. racemosus*

Populus tremuloides, Pteris aquilina and *Symphoricarpos racemosus* range over a very wide area. The remaining species are exclusively western and are mostly typical Rocky Mountain plants.

A number of fossils appear to be closely related to present day northern Rocky Mountain plants not found near the fossil bed. Some of these living species grow in low areas of the panhandle region of Idaho or in higher elevations throughout the Rockies. Many occur generally in southwestern Idaho.

Fossil species	Similar living species
Alnus corrallina	*A. rhombifolia* Nutt.
Alnus carpinoides	*A. sinuata* (Regel) Rydb.
Cercocarpus cuneatus	*C. montanus* Raf.
Picea lahontensis	*P. Engelmannii* (Parry) Engelm.
Pinus quinifolia	*P. monticola* Dougl.
Prunus covea	*P. emarginata* (Dougl.) Walp.
Salix spokanensis	*S. commutata* Bebb
Salix Schimperi	*S. cordata* Muhl.
Thuja Garmani	*T. plicata* D. Don

This very marked similarity between twenty species of the fossil and living floras of Thorn Creek and vicinity indicates that a flora closely similar in certain respects to the modern Rocky Mountain flora was present in that region as early as Tertiary times. In addition, it contained elements indicating a climate distinctly more humid. It would appear that the commonest fossil species were of eastern affinity and have become extinct in the West without leaving descendents, whereas the already differentiated western element of the fossil flora consisted principally of species that have left living descendents in the same general region.

The largest percentage of actual specimens fall in the group of species with supposed living equivalents in the northeastern states and in the Appalachian region. Since the preliminary account (34) of Thorn Creek fossils with supposed living equivalents in the eastern United States was written, several additional species have been added to that category. The range of some of these plants extends into the southeastern Atlantic states. The revised list follows:

Fossil species	Similar living species
Acer negundoides	**A. Negundo* L.
Acer Osmonti	*A. saccharinum* L.
Betula idahoensis	*B. lenta* L.
Carpinus payettensis	*C. carolinana* Walt.
Carya egregia	*C. ovata* K. Koch
Fagus pacifica	*F. grandifolia* Ehrh.
Fraxinus leptocarya	*F. quadrangulata* Michx.?
Magnolia oregoniana	*M. virginiana* L.
Populus Booneana	**P. tremuloides* Michx.
Populus washoensis	*P. grandidentata* Michx.
Prunus Chaneyi	*P. serotina* Ehrh.
Pteris calabazensis	**P. aquilina* L.
Quercus Bretzi	*Q. bicolor* Willd.
Quercus Eoprinus	*Q. Prinus* L. (*Q. montana* Michx.)
Quercus Maccanni	*Q. bicolor* Willd.
Quercus Merriami	*Q. rubra* L.
Quercus payettensis	*Q. Muhlenbergii* Engelm.
Rhododendron idahoensis	*R. maximum* L.
Salix Schimperi	**S. cordata* Muhl.
Symphoricarpos elegans	**S. racemosus* Michx.
Tilia parvulifolia	*T. floridana* Small
Ulmus paucidentata	*U. alata* Michx.

The species marked with an asterisk are of wide distribution and are not necessarily characteristic of the flora of the eastern United States. *Betula, Populus, Prunus, Rhododendron* and *Fraxinus* occur in both eastern and western United States. The first three are found in southwestern Idaho, mostly as stream border plants. Thus, *Carpinus, Carya, Fagus, Magnolia,* five species of *Quercus, Tilia* and *Ulmus* are the really characteristic eastern American representatives. It is curious that whereas *Fagus pacifica* and *Quercus Eoprinus* are the numerical dominants in the flora and the *Ulmus* is well represented, the other nine species are now known from only a few specimens. This may be because the collections all came from a single locality. Collections from a neighboring fossil bed, if one could be found, might have a somewhat different numerical distribution. *Fagus* of the *F. grandifolia* type grew over a considerable part of the northwest during the Miocene, but neither its principal ecological associate at Thorn Creek, *Quercus Eoprinus,* nor a closely similar species has been reported associated with it elsewhere. Several common members of the eastern hardwood association are not included in this flora. *Castanea, Nyssa, Liriodendron, Liquidamber* and *Sassafras* have not been reported from various nearby Miocene floras, but so far as is now known, they are absent from Thorn Creek.

A number of the fossil species have living representatives now growing in the humid Pacific Coast regions.

Fossil species	Similar living species
Acer glabroides	**A. glabrum* Torr.
Acer negundoides	**A. Negundo* L. and varieties
Alnus corrallina	**A. rhombifolia* Nutt.
Alnus carpinoides	**A. sinuata* (Regel) Rydb.
Amelanchier dignata	**A. alnifolia* Nutt.
Arbutus Matthesii	*A. Menziesii* Pursh
Castanopsis angustifolia	**C. chrysophylla* DC.
Populus Booneana	**P. tremuloides* Michx.
Populus eotremuloides	**P. trichocarpa* T. & G.
Prunus covea	**P. emarginata* Walp.
Pseudotsuga Masoni	**P. taxifolia* (Poir.) Britt.
Pteris calabazensis	**P. aquilina* L.
Quercus Browni	*Q. chrysolepis* Liebm.
Quercus pseudolyrata	*Q. Kelloggi* Newb.
Rhamnus idahoensis	**R. Purshiana* DC.
Salix Schimperi	**S. cordata* Muhl.
Salix boisiensis	**S. Scouleriana* Barr.
Salix venosiuscula	**S. lasiandra* Benth.
Sequoia Langsdorfii	*S. sempervirens* Endl.
Symphoricarpos elegans	**S. racemosus* Michx.
Thuja Garmani	**T. plicata* D. Don

As in the previous list the asterisk means that the living species is not confined to the area mentioned. It is clear from the above list that no really typical redwood or redwood border element (association) was important at Thorn Creek at the time of the deposition of these sediments. Of the species confined to the coastal region one, *Q. Kelloggi,* may not necessarily be the most similar living equivalent for the fossil form. There are two or three eastern American black oaks that also closely resemble *Q. pseudolyrata. Sequoia* of

the coast redwood type is represented by only a few specimens. *Arbutus Mat*-thesii is likewise sparcely represented. *Q. Browni*, having as its living equivalent *Q. chrysolepis*, is suggestive of some of the Coast Range associations. The almost total absence of the ecological associates of redwood is in contrast with many of the earlier Miocene floras and serves to place the probable age of the Thorn Creek flora in the middle or late Miocene.

The southwestern element is small and includes mostly semi-chaparral species and a few that are widespread or occur in some of the other regions mentioned.

Fossil species	Similar living species
Acer negundoides	**A. Negundo* L.
Arbutus opaca	*A. glandulosa* M. & G.
Cercocarpus cuneatus	**C. montanus* Raf.
Diospyros elliptica	*D. Texana* Scheele
Populus Booneana	**P. tremuloides* Michx.
Pseudotsuga Masoni	**P. taxifolia* (Poir.) Britt.
Pteris calabazensis	**P. aquilina* L.
Quercus boisiensis	*Q. Eastwoodiae* Rydb.
Quercus simulata	*Q. hypoleuca* Engelm.?
Quercus Tuckeri	*Q. annulata* Sarg.
Sapindus idahoensis	*S. Drummondii* Hook. & Arn.

Almost half of these living species are found in other regions. The box elder, quaking aspen and bracken are widely distributed. *Cercocarpus* and *Pseudotsuga* are common in the western flora. The latter reaches the southern limit of its distribution in the mountains of northern Mexico. None of these can be considered as characteristic of any one region or any particular set of climatic conditions except that they grow in the drier parts of the various mesophytic regions.

The remaining species definitely suggest a scrubby forest dominated by oak and madrone. This type of association is encountered in some of the inner Coast Ranges of northern California as well as in the mountains of Mexico. A vegetation without the madrone, but of probably similar aspect, is found in the Wasatch Mountains east of Salt Lake City, Utah. *Sapindus, Diospyros* and *Cercocarpus*, growing as they do as scattered trees, scrubby trees or shrubs in fairly dry subchaparral habitats, are not unlikely additions to such an association. It seems reasonably safe to assume that such an association, with the possible addition of *Quercus clarnensis*, occupied the drier ridges and south-facing slopes around the bed of deposition.

The affinity between certain western Miocene oaks and those from the southwest and northern Mexico has been previously pointed out by Berry (5). Although growing in an arid region, these living equivalents usually grow in canyons or near streams where there is at least a moderate supply of water. According to a written note (unpublished) by Professor H. H. Bartlett:

> Collectors in arid portions of Mexico frequently have the experience of turning up species of highly restricted and localized distribution as relicts of an old mesophytic vegetation in deep ravines, near mountain streams and along rills. As an example one may cite a typical hickory and an elm related to the group of *Ulmus americana* which maintain a most precarious existence in isolated bits of mesophytic habitat in the moun-

tains of Tamaulipas and Nuevo Leon. This hickory, particularly, could in no way span the desert stretches that lie between the isolated and small areas where it grows. Here we have an example of the dying out, not yet complete, of species in arid Mexico which may in former geological times have extended much farther to the westward.

Ecological Considerations

On the basis of the habitats of the supposed living equivalents an area of considerable altitudinal range is indicated by the fossil plant assemblage. Certain of the supposedly equivalent living species are characteristic of high altitudes and grow usually above 5000 feet either in the Rocky Mountains or Sierra Nevadas or both. Other species are restricted to wet or swampy places in lower elevations. A third group intermediate between these two is recognized and includes species of uplands and fairly dry ridges.

Certain plants, such as *Pseudotsuga* and *Pteris*, are found from sea level up to great elevations. Because of its scarcity in this fossil record the former is here considered to have been growing in the higher mountains and was consequently at some distance from the place of deposition. The *Pteris* appears to be more similar to those specimens which grow under somewhat xerophytic conditions than to the specimens which grow in the humid coastal regions. The following list enumerates those species in the fossil flora that may have been characteristic of high elevations.

Abies laticarpa
Abies parviseminis
Acer glabroides
Alnus carpinoides
Alnus corrallina
Amelanchier dignata
Amelanchier subserrata
Betula lacustris
Picea lahontensis
Pinus quinifolia
Populus Booneana
Populus dolichophylla
Populus eotremuloides
Pseudotsuga Masoni
Salix Schimperi
Salix spokanensis
Salix venosiuscula
Sequoia affinis

All of the above species except *P. eotremuloides* are meagerly represented as is quite in keeping with their postulated growth at high altitudes. The leaves of *P. eotremuloides* appear to be moderate in size and fairly thick. They are suggestive of leaves of the living *P. trichocarpa* as it is found at Thorn Creek. Leaves of this species from humid coastal areas are larger and thinner. The other species of *Populus* and *Alnus* are not necessarily restricted to high altitudes, but since they are surprisingly poorly represented, it is probable that they were growing either at higher elevations some distance from the place of deposition or as scattered individuals. This sparse representation is in decided contrast to certain species from some of the other groups.

The largest number of species belong to the group that apparently grew at intermediate elevations. Two elements can be recognized, the semi-chaparral and the mesophytic hardwood species. The following list enumerates the supposed xero-mesophytic semi-chaparral species.

Arbutus opaca
Cercocarpus cuneatus
Diospyros elliptica
Quercus boisiensis
Quercus simulata
Quercus Tuckeri
Sapindus idahoensis
Ulmus paucidentata

The second list includes mesophytic hardwood species which seem more associable with the flora of eastern America than with the semi-chaparral element. These species of eastern aspect probably occupied the more mesophytic parts of areas that were becoming, even in the Miocene, semi-arid and in which the immigration of chaparral species had begun. The latter may be presumed to have gained ascendency as the eastern element dwindled and eventually became extinct. The evidence that there was a beech-maple association would indicate ecological conditions not unlike those that characterize the region of beech-maple climax forest in the eastern states. We may tentatively conclude that this beech-maple climax was being succeeded by a new semi-chaparral climax as a result of increasing dryness. In other words, beech-maple forest at the time of deposition of the beds ceased to be the wide-spread climatic climax of the region and was on the wane. It probably existed only in favored localities, such as in a locality in the eastern Sierra Madre of Mexico where S. S. White* has found a typically Alleghanian-Ozarkian flora which persists as a relic in a wet canyon surrounded by a region of subdesert vegetation. H. H. Bartlett* found a similar localized florula in the San Carlos Mountains of Tamaulipas. The mesophytic species follow:

Acer negundoides
Betula idahoensis
Carya egregia
Castanopsis angustifolia
Fagus pacifica
Fraxinus leptocarya
Pteris calabazensis
Quercus Eoprinus
Quercus Merriami
Quercus payettensis
Quercus pseudolyrata
Rhamnus idahoensis
Sequoia Langsdorfii

A few species may have been typically lowland and two or three others may be considered either intermediate or lowland.

Carpinus payettensis
Castanopsis angustifolia
Magnolia oregoniana
Quercus Bretzi
Rhododendron idahoensis
Tilia parvulifolia
Thuja Garmani

The living equivalents of this group grow on moist bottom lands, along streams or in low swampy places and usually are not found at higher elevations. *Carpinus, Magnolia* and swamp chestnut oaks no longer occur in the West. None of this group is well represented in the fossil flora.

It is evident from the geographic distribution of the living equivalents that the Thorn Creek flora grew in an area of considerable topographic relief. The topography may have been much the same as it is in the Boise Basin today, that is, fairly broad valleys surrounded by high mountains. The majority of the plants represented as impressions grew in the basin or low valleys, others were found on the low hills and the conifers grew on the high mountains. The precipitation was probably not less than thirty inches annually, and there was no pronounced summer dry season such as now prevails in that region. The temperature, except on the high mountains, was probably not extreme and not subject to great variation.

* Oral communication of H. H. Bartlett, April, 1940.

Comparison with Other Fossil Floras

Table 3 shows the distribution of the species of fossil plants found at Thorn Creek in certain other western fossil beds. However, the value of such a chart is somewhat limited. Because of the different methods of interpreting fossil species followed by various paleobotanists, such a table does not give an adequate picture of the ecological similarities between two floras. Perhaps more important, it does not emphasize all of the significant differences. For these reasons a brief discussion of the associations and numerical dominants where reported, may prove to be at least as significant, if not more so, than a mere numerical comparison of the number of similar species reported from various floras.

In Lindgren's original collection of Payette plants thirty-two species were enumerated. Because of the doubtful determinations and inadequate illustrations, systematic and consequently ecological relationships between the original Payette flora and that of Thorn Creek are hard to determine. It is hardly likely that the generic determinations of *Ficus, Celastrus, Rhus* and *Myrica* are correct. Three of the Thorn Creek species, *Populus eotremuloides, Quercus simulata* and *Q. payettensis,* were included in the original collection of Payette plants. It is highly probable that *Sequoia angustifolia?, Myrica? idahoensis, Populus occidentalis, Platanus aspera?, Celastrus Lindgreni* and *Acer trilobatum productum?* are the same as *Sequoia Langsdorfii, Arbutus idahoensis, Populus oetremuloides, Acer glabroides, Populus dolichophylla* and *Acer glabroides* respectively of the Thorn Creek flora. It is likely that a study of the actual collections would show a greater number of identities.

The Sucker Creek flora is not as homogenous as is that from Thorn Creek. Neither is it so clearly related to any one modern flora. *Quercus* is the dominant genus in both with seven species reported from the former and twelve from the latter. There is a distinct difference in the type of oaks represented. The Sucker Creek beds have almost exclusively narrow, rather coriaceous-leaved species, whereas Thorn Creek in general has broad, apparently thin-leaved species. Moreover, two species of *Castanea* and *Castanopsis* have been reported from Sucker Creek, the latter being very abundant. *Castanea* is apparently not present at Thorn Creek whereas *Castanopsis* is represented by a new species. *Fagus* at Sucker Creek is rather rare, as are willows. *Platanus* is very abundant and three species have been reported. Four species of fossil *Mahonia* are known from Sucker Creek, but no fossil record of the genus has yet been found at Thorn Creek where a living species is growing just above the fossil bed. *Pinus* is found in both floras, but is represented by totally different types. At Sucker Creek the three-needled *P. Knowltoni* (presumably related to the modern yellow pines) is common in certain localities, whereas the Thorn Creek *Pinus* is a five-needled one (i. e., a white pine). Only two fern fragments have been found at Thorn Creek. There is a whole ledge of *Woodwardia deflexipinna* at Sucker Creek near Rockville, Oregon. Fern fragments have not been observed from the other Sucker Creek localities, however.

Of the fifty-eight Sucker Creek species which I (35) have recognized, eighteen have living equivalents in the western United States, only a few of

TABLE 3.—Distribution of Thorn Creek species in some other western Tertiary floras.

	Lower Miocene		Middle or Upper Miocene								Transitional or Pliocene		
*	1	2	3	4	5	6	7	8	9	10	11	12	13
Abies laticarpa					×	×	×						
Abies parviseminis							×						
Acer glabroides	×		×			×	×		×	×	×		
Acer negundoides			×	×	×		×			×	×		
Acer Osmonti				×					?	×			
Acer Scottiae					×						×		
Alnus carpinoides	×		×		×	×	×			×			
Alnus corrallina			×					×			×		
Amelanchier dignata				×	×						×		
Arbutus idahoensis			×		×	×			×	×	×		
Arbutus Matthesii	×						×						
Betula lacustris					×								
Carya egregia			×			×	×			×			
Cedrela pteriformis			×										
Cercocarpus cuneatus													×
Craetaegus microcarpifolia					×								
Diospyros elliptica				×									
Fagus pacifica	×	?	×			×	×			×			
Magnolia oregoniana		×											
Picea lahontensis					×						×		
Populus eotremuloides			×				×		×	×			
Populus washoensis							×			×			
Prunus Chaneyi								×					
Prunus covea	×					×				×			
Pseudotsuga Masoni					×		?				×		
Pteris calabazensis													×
Quercus Bretzi		×	×										
Quercus clarnensis	×												
Quercus Maccannii			×								×		
Quercus Merriami		×	×	×									
Quercus payettensis			×						×				
Quercus pseudolyrata		×		×		×	×						
Quercus simulata		×	×		×	×	×		×	×	×	×	
Rhamnus idahoensis			×										
Salix spokanensis			×										
Sequoia affinis												×	
Sequoia Langsdorfii	×		×	×			×		×	×	×	×	
Symphoricarpos elegans										×	×		
Thuja Garmani											×	×	
	7	5	17	7	11	9	13	2	6	13	13	3	2

* See page 487 for explanation.

which are associates of the modern redwood. In both floras *Sequoia* is rare. Nineteen Sucker Creek species have closely related living equivalents in the eastern United States. Several of these are in the genera *Ulmus, Sassafras, Ostrya, Nyssa, Fagus* and *Carya* now extinct in the West. In contrast to the Thorn Creek flora that of Sucker Creek has an eastern Asiatic element of some importance, comprising ten species and including three genera that do not occur naturally in the United States.

From a comparison of these two neighboring fossil florulas (both of which are probably Payette) it seems evident that, on the basis of present knowledge, the Sucker Creek florula is more cosmopolitan. It must, however, be borne in mind that this florula has been collected from numerous localities, some of which are separated by twenty-five or thirty miles, whereas the Thorn Creek specimens were all taken from a single outcrop.

Other nearby fossil beds are the Idaho beds near Weiser, Idaho. Dorf (16) has pointed out the similarity of this flora to that of the *Lithocarpus-Quercus-Arbutus* community of the inner Coast Ranges of California. The most important species numerically were listed as *Typha Lesquereuxi, Quercus simulata, Acer negundoides, Salix coalingensis* and *Juniperus sabinoides*. None of these is dominant at Thorn Creek and several do not even occur there so far as is now known. Six species of *Quercus* were reported, but the broad-leaved black oaks and the chestnut oaks so common at Thorn Creek are either scarce or lacking.

The two floras have several points of similarity not brought out in the table. Both, for instance, have *Fraxinus* samaras, small *Ulmus* leaves, *Ulmus* fruits, *Abies* fragments, *Cercocarpus* leaves and *Pinus* needles, which although now considered specifically distinct may not all be so. Only a few Weiser species have living equivalents in eastern Asia, and only a few have living representatives confined to the eastern United States.

The Blue Mountain flora as published by Oliver (29) on collections from Tipton and Austin, Oregon, comprises thirty-two species. Of the seven conifers, *Sequoia Langsdorfii* and *Pinus Knowltoni* are abundant. Three elements were observed, (1), the Pacific Coast element of twenty species which included both redwood and non-redwood associates; (2), Appalachian element of seven species; and (3) the eastern Asiatic element. In contrast to the Thorn Creek flora, the small non-lobed oaks are abundant and only *Q. pseudolyrata* represents the broad leaved species. *Platanus* and a large-leaved *Acer* are found in the Blue Mountain flora. It is evident that these two floras could not have been very similar in aspect even though they have eleven species in common.

The Trout Creek flora of south central Oregon, like that of Thorn Creek,

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* 1, Bridge Creek; 2, Eagle Creek; 3, Latah of Wash. and n. Idaho; 4, Mascall, John Day Basin; 5, Trout Creek; 6, Blue Mountains; 7, Upper Cedarville; 8, San Pablo; 9, Type Payette; 10, Sucker Creek; 11, Weiser; 12, Linson Valley, Idaho; 13, Pliocene, California.

resembles a modern flora of the western mountains. However, the vegetation of the Klamath Mountains, which the former resembles, differs in many respects from that of the northern and central Rockies. According to MacGinitie (28) the numerical dominants of the fossil flora are tan oak, madrone, Douglas fir and Port Orford Cedar equivalents. There is also a considerable Asiatic element. From this it is evident that the two fossil floras are quite dissimilar.

Fourteen Thorn Creek species have been reported from the Latah formation of Washington and northern Idaho. If a careful comparison of nearly similar species were made this resemblance would undoubtedly be increased. It is probable that *Pinus tetrafolia* is the same as *P. quinifolia,* that *Pteris* sp. is a form of *P. aquilina* and the same as *P. calabazensis* from Thorn Creek,etc. With the large representation of *Fagaceae, Salicaceae* and *Betulaceae,* the Latah flora must have had a facies somewhat like that of Thorn Creek. The former flora contains over one hundred and fifty species and is the largest of those considered here.

According to Berry (5) the most numerous leaves are those of oaks, poplars, redwood and bald cypress. In discussing the flora he wrote, "The Latah flora is an overwhelmingly temperate flora entirely appropriate to the latitude where it is found, and indicative of an ample, well distributed rainfall of possibly between 30 and 40 inches annually. It is rather closely paralleled among existing floras by those of such a Middle Atlantic State as Maryland." This flora must have lived under moister conditions than the Sucker Creek and Thorn Creek floras since *Sequoia and Taxodium* are abundant in it.

The Upper Cedarville flora of northwestern Nevada and adjacent California as presented by LaMotte (24) consists of forty-six species. *Typha Lesquereuxi, Sapindus oregonianus* and *Carya egregia* constitute 55 percent of the total number of impressions. None of these is numerically important at Thorn Creek although *Fagus pacifica* which is sixth in the Upper Cedarville is second in the Thorn Creek collection and *Quercus simulata* and *Carya egregia* are present in small numbers. LaMotte found that over 65 per cent of the nearest living equivalents are to be found in the present flora of the west coast. Second in importance are those species with living equivalents in eastern Asia. A smaller number are represented in the eastern United States.

The main climax association is supposed to have been an oak-hickory-beech association suggestive of the hardwood forests of eastern Asia and eastern America. The flora as a whole indicates a cool climate with no summer dry season and considerable precipitation. The climax association is quite similar to that of Thorn Creek in the importance of oak, maple and beech.

There is scarcely any similarity between the Thorn Creek and San Pablo floras as they are now known. The latter, which is considered to be Upper Miocene, is found in California around San Francisco Bay. Condit (15) reported it as a small flora of twenty-six species. The dominant element is the *Taxodium-Nyssa* association which now occurs in the deep swamps of the southeastern coastal plain.

The lack of similarity between these fossil floras is to be expected because of the great distance separating them and because of the probably great difference in climatic conditions. There may also be some age difference, but it is not necessary to assume that this is true, since exactly the same floristic differences could easily be found today between southeastern localities not too distant, one in the Appalachian Mountains and one in the coastal plain, or one in the Ozark uplift and one in the lower Mississippi Valley.

In many respects the Eagle Creek flora is similar to that of Thorn Creek. They both have a wealth of broad-leaved oaks, and include *Fagus,* small-leaved elms, poplars of the *P. tremuloides* type, *Alnus, Betula, Carya, Crataegus, Tilia, Prunus,* etc. A more detailed comparison of the specimens and species than it is feasible for me to make might well show a much greater degree of similarity than is now indicated by the five species in common. As suggested by Chaney (12) and indicated in his chart showing the distribution of the modern equivalents of the Eagle Creek plants, they occupy the eastern United States where they are important members of the mesophytic hardwood forests. One point of dissimilarity is of special interest, namely, the absence of the modern Rocky Mountain element in the Eagle Creek and its presence in the Thorn Creek flora. This may be ascribed to the geographic positions of the two floras or to the fact that during Eagle Creek time the northern Rocky Mountain element was still farther to the north. This element, although present in some other fossil floras, has received little emphasis and may be of greater importance than is now generally recognized.

The Eagle Creek flora is like that of Thorn Creek in that only a few species have living equivalents confined to eastern Asia. It is also interesting to note the absence of *Platanus* at Eagle Creek, Trout Creek, the Upper Cedarville formation and Thorn Creek. Just what importance can be attached to its absence I am not prepared to say, but it is interesting because of the marked abundance of the genus in so many western Miocene floras.

The lower Miocene Bridge Creek flora of the Crooked River Basin of Oregon has been studied by Chaney (14). He found it to be like the modern redwood forest with 48 per cent of the species being redwood associates. The non-redwood western element and the eastern American element are of about equal importance, the first including 16 and the second 18 per cent of the species. The Asiatic element and those species of uncertain affinities are of minor importance. The four numerical dominants are reported as *Quercus clarnensis, Alnus carpinoides, Typha Lesquereuxi* and *Sequoia Langsdorfii.* Of these, the last three are represented by only a few specimens each at Thorn Creek. *Q. clarnensis,* however, is quite well represented.

Chaney made only generic comparisons between the fossil and living floras of Bridge Creek and vicinity. He found that twenty of the thirty-nine genera present in the fossil flora are still living in the general region of the Crooked River Basin and Blue Mountains, Oregon. It is evident that the Bridge Creek and Thorn Creek floras were quite dissimilar although there are several likenesses not brought out in the table. The small *Ulmus Brownelli* is quite similar

to *U. paucidentata*. *Crataegus Newberryi* and *C. microcarpifolia* are known only from isolated leaf impressions and may well represent a single species.

It seems likely that the Bridge Creek beds preserve a record of a habitat in which the mesophytic climatic climax had not yet been attained since *Sequoia* was dominant and *Fagus* rare. In contrast to this at Thorn Creek the climax vegetation of eastern type had been obtained and as a result of increasing aridity, was disappearing. In its place the Rocky Mountain element of the present day was coming in. This succession is quite in keeping with the supposed age relations of the two floras, the Bridge Creek is older and should, therefore, represent an earlier phase of ecological succession than the Thorn Creek flora.

From the foregoing discussion it is evident that as far as the interpretation of the ecology of the various floras is concerned, the general aspect of the Thorn Creek is in many ways distinct from them all, but that its general facies is more like the Latah flora of northern Idaho and Washington, the Upper Cedarville of Nevada and California and the Eagle Creek of the Columbia River Gorge, Oregon, than any others.

Age of the Flora

The stratigraphic occurrence of the plant bed in an intermontane basin in southwestern Idaho and its proximity to the type localities of the Payette formation suggest that this is another outcrop of that formation and would, therefore, now be considered Upper Miocene in age. The distribution of the species in other formations of supposed Upper Miocene age also bears out this assignment.

Systematic Descriptions of Species

Species for which no comments are needed are omitted from this list. The complete list of species has been given on page 475. The fossil flora as reported in this paper includes sixty-four named species and eight that are not given specific names. These are distributed among thirty-six genera in twenty families. Only one fern is included. Six genera of the Spermatophyta are gymnosperms. Two monocotyledons have been recognized, one of which is too fragmentary for identification. A representative collection of the fossils has been deposited in the Museum of the University of Notre Dame. Type specimens only are in the Museum of Paleontology of the University of Michigan.

Pinaceae

Pinus quinifolia n. sp. Plate 2, figs. 2, 8. Needles slender, in clusters of five; sheath either absent or very inconspicuous; length of needles quite constant, about 4.5-5 cm. Type no. 21456 U. M.

A somewhat similar fascicle containing only four needles was described as *P. tetrafolia* by Berry (5). This name was based upon a single specimen and has subsequently been applied to a fossil from Weiser, Idaho. Because the typical needle number (five) shows that the Thorn Creek specimens belong to the white pines, they are described here as new although it is probable that the Latah specimens also represent a five-needled or white pine in which the fifth needle either does not show or was lost before fossilisation. In any event, it seems best to describe species on the basis of really adequate material whenever it is possible to do so.

PLATE 2

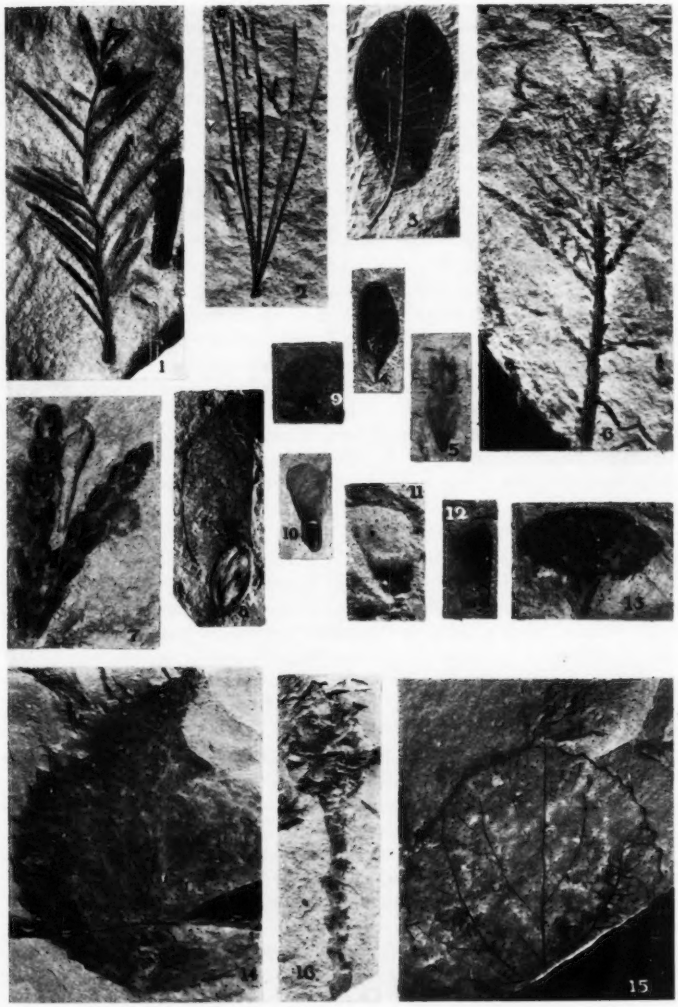


Fig. 1. *Sequoia Langsdorfii* (Brongn.) Heer. Figs. 2, 8. *Pinus quinifolia* n. sp. Fig. 2 type, no. 21456 U. M. Fig. 3. *Salix boisiensis* n. sp. Type no. 21466 U. M. Figs. 4, 5. *Pseudotsuga Masoni* MacG. Fig. 6. *Sequoia affinis* Lesq. Fig. 7. *Thuja Garmani* Lesq. ×2½. Fig. 9. *Abies parviseminis* LaMotte. Fig. 10. Unidentified seed. Fig. 11. *Abies laticarpa* MacG. Fig. 12. *Pinus* sp. seed. Fig. 13. *Abies* sp. cone scale. Figs. 14, 15. *Populus Booneana* n. sp. Fig. 15 type, no. 21462 U. M. Fig. 16. Unidentified cone.

Several species of white pine have been reported from the western Miocene. *Pinus* sp. Knowlton from near Ashland, Oregon, has needles that are both longer and stouter than *P. quinifolia*. *P. latahensis* Berry from the Latah formation of Republic, Washington, is even larger, having needles at least 9 cm. long. Brown (10) has reported a five-needled pine with needles 3-4 cm. long from Thunder Mountain, Idaho. It is probable that this is the same species as the Thorn Creek material. *P. Wheeleri* Cockerell from Florissant, *P. Torreyana* Parry (a living 5-needled yellow pine supposed to be associated with *Sequoia Langsdorfii* and *Alnus carpinoides* at Bridge Creek (Mason, 27)) and *P. monticolensis* Berry from the Latah are all 5-needled pines with longer and usually considerably stouter needles than the Thorn Creek fossils.

Among living species, *P. monticola* Dougl. and *P. Strobus* L. have leaves that are quite similar to the fossils but they may be much longer also. *P. albicaulis* Engelm. and *P. aristata* Engelm. have shorter needles which are stouter and tend to be more curved. *P. flexilis* James is almost identical in needle size but apparently the needles are more rigid. *P. monticola* is probably the nearest living equivalent of this fossil species in spite of the great variation in length of the needles. They may vary up to three or four times the observed length of the Thorn Creek fossils. This western white pine grows in the higher mountains from British Columbia to the Sierra Nevadas and extends eastward into Idaho and Montana. Its altitudinal range is great for it occurs from sea level up to 10,000 feet.

Pinus sp. seed. Plate 2, fig. 12. Seed with wing a little over 1.3 cm., seed round, 4 mm. in diameter; wing broadly strap shaped, flaring slightly for two-thirds of its length, inner margin straight to just below the apex where it curves concavely; outer margin slightly convex, then narrowed abruptly in the apical third; width of wing at point of attachment to seed 5.5 mm., at widest point 6 mm., length 1.3 cm.

In size and shape these seeds rather closely resemble P. *aristata* Engelm., the foxtail pine, which grows on rocky and gravelly slopes at the upper limit of tree growth in the Rocky Mountains.

Pseudotsuga Masoni MacG. Plate 2, figs. 4, 5. A bract and a few winged seeds are the representatives of this species. Bract 1.75 cm. long, two lateral lobes at the apex; midrib strong, extending out to form a rigid needle-like point; bract slightly constricted above the middle.

The only discernable difference between this bract and those of the living *P. taxifolia* is in the slightly smaller size of the fossil. The Douglas fir is found throughout the Rocky Mountains of the United States and occurs over a wide altitudinal range.

Abies laticarpa MacG. Plate 2, fig. 11. A single elongate seed about 2 mm. wide and 4 mm. long with an expanded wing may be referred to this species. It differs from the Trout Creek specimen illustrated by MacGinitie (28) in having a narrower wing.

Abies magnifica var. *shastensis* Lemm., a living species reported from the John Day beds by Mason (27), is also somewhat similar but the wing is shorter.

Several living species, *Abies grandis* Murr., *A. concolor* (Gord.) Parry and *A. grandis* Lindl., have seeds quite similar to the fossils.

Abies parviseminis LaMotte. Plate 2, fig. 9. A single small, almost quadrangular seed with a deltoid wing is the only representative of this species. Among living plants the seeds of *A. lasiocarpa* (Hook.) Nutt. are quite similar. This balsam fir is found from Alaska through the mountains to Oregon and in the Rockies south to Arizona.

Abies sp. (cone scale). Plate 2, fig. 13. Several cone scales suggestive of those of *Abies* are included in the collection. They are not at present assigned to either of the seed species although they probably represent at least one of them. The scales are quite like those of *A. concolor* so should, perhaps, be referred to *A. laticarpa.*

Sequoia affinis Lesq. Plate 2, fig. 6. (New classification *Sequoiadendron affinis*). Several specimens of these slender, much branched twigs clearly indicate the places for abcission of the small deciduous lateral branches. The big tree, *Sequoia gigantea* Decne., has branches of exactly the same kind. This living species, like the redwood has a very restricted range, in fact, its range is even more restricted. It is known from about thirty-two groves scattered along the western slope of the Sierra Nevadas. The temperature range endured is quite wide, from -12° to 100° F. It is evident that the big tree exists under considerably harsher conditions than does the redwood, and its occurrence at Thorn Creek is of particular interest because of the climatic implications. The indicated climate is quite in keeping with the postulated requirements of the dominant species in the Thorn Creek flora.

Except for Kirkham's collections from Linson Valley (18), there has been no definite record of *S. affinis* from southwestern Idaho or eastern Oregon. Lindgren (26) did, however, mention two species as *"Sequoia sp.* like *S. gigantea"* from Sucker Creek, Oregon. Neither figures nor descriptions were given so it is impossible to express any opinion as to their similarity to the Thorn Creek specimens.

Sequoia Langsdorfii (Brongn.) Heer. Plate 2, fig. 1. A few small, deciduous, lateral branches like those of the coast redwood, *Sequoia sempervirens* Endl. were found. One has a small bud at the end and shows clearly the smaller leaves characteristic of the base of a branchlet. At the present time the redwood is confined to a narrow belt on the western slope of the Coast Ranges of California. *Sequoia* had a wide distribution in the early Tertiary and is quite abundant in such formations as the Bridge Creek. The progressive aridity and greater temperature differences in later Miocene times greatly restricted its range and only a few scattered areas indicate its wider extent then and during the Pliocene. Because of the extreme sensitivity of the living species to environmental conditions, *Sequoia* is taken to be a good indicator of past climates. It was apparently rare in southwestern Idaho and eastern Oregon during Miocene and early Pliocene times. Such specimens as remained in the Thorn Creek flora were probably a few survivors in favored locations.

Thuja Garmani Lesq. Plate 2, fig. 7. Three small specimens are assigned

to this species. It is difficult to distinguish *Thuja* from *Chamaecyparis* on the basis of leafy shoots alone. The reference of these specimens to *T. Garmani* is based upon their similarity to *T. plicata* D. Don and to the fossil from Weiser, Idaho, figured as *T. Garmani* by Dorf (16).

The western red cedar ranges from sea level to elevations of 6000 feet along the western side of the continental divide in the northern states. It occurs widely in swamps in the Olympic region of Washington and singly and in small groves from Alaska to northern California. *T. Garmani* might almost equally well be considered similar to *T. occidentalis* L., the white cedar or arbor-vitae, of the northeastern United States and Appalachian region.

Salicaceae

Populus Booneana n. sp. Plate 2, figs. 14, 15. Leaves suborbicular with a short acuminate apex; base broadly cuneate; margin crenate; the rounded teeth usually pointing outward; midrib straight or flexuous; secondaries 4-6 pairs, usually alternate, some intermediates present; lowest secondaries giving off 4 or 5 abaxial veins, some of which fork as do the secondaries; tertiary venation irregular; ultimate venation a coarse reticulum; texture membranaceous. Type no. 21462 U. M.

This species is characterized by the almost round shape and the short acuminate apex of the leaf. Three principal veins arise from the top of the petiole but two additional weak ones may be present.

Of the living species studied, *P. rotundifolia* from the Himalayas is quite similar. Among American species, *P. tremuloides* is most like the fossil. The quaking aspen is common in the mountains of Idaho and was found growing along Thorn Creek. It is frequent in the higher elevations and colder regions of North America.

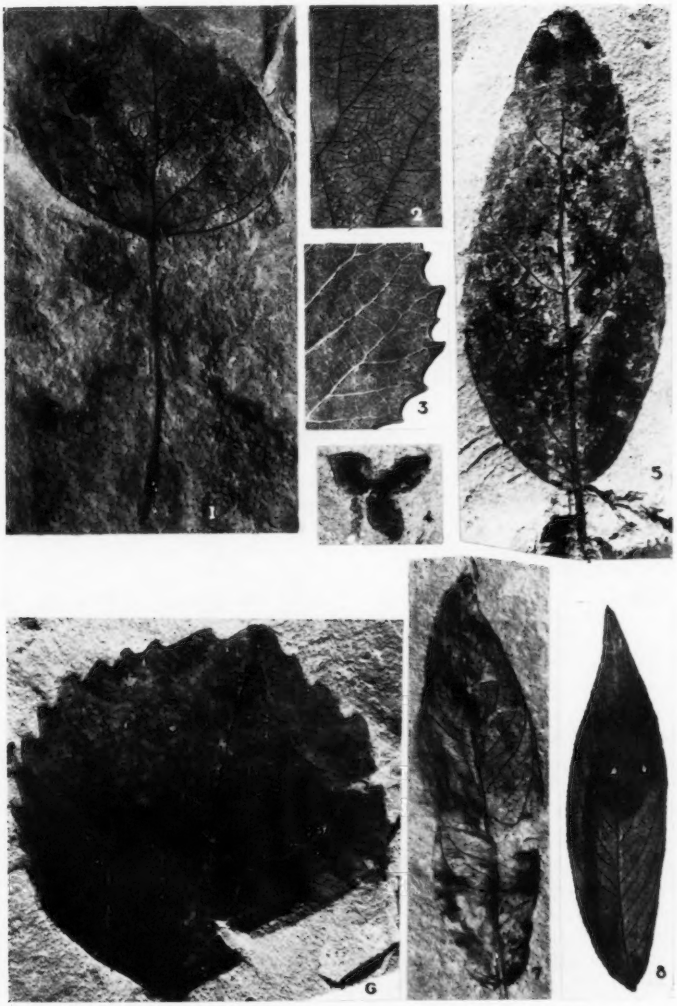
This species is named in honor of the late Dr. W. J. Boone of the College of Idaho, a pioneer botanist of Idaho.

Populus dolichophylla n. sp. Plate 3, fig. 5; plate 4, figs. 1, 2, 4. Leaves ovate-lanceolate to narrowly lanceolate, 3.5-9 cm. long, 1-3.5 cm. wide, widest in the lowest third and narrowing to a long acuminate apex and narrow cuneate base; margin finely and regularly crenate-serrate except at the entire base; teeth small, forward pointing; midrib moderately stout, often flexuous or curved; secondaries thin, alternate, over seven pairs, those in the extreme upper part of the blade indistinct, all arching upward near the margin, often giving off adaxial tertiaries that form loops with the next secondaries above, some, especially the lowest pair, giving off a few abaxial tertiaries which extend out to end in arches just within the margin; tertiary venation consisting of some percurrent tertiaries almost perpendicular to the midrib; ultimate venation an irregular reticulum. Type no. 21459 U. M.

The leaves which Knowlton (21) figured and described as *Celastrus Lindgreni* from the type Payette formation appear to be this species.

P. dolichophylla is another Thorn Creek fossil species which has its supposed living representative still growing in that locality. *P. angustifolia* James

PLATE 3



Figs. 1, 2, 6. *Populus washoensis* Brown. Fig. 3. Portion of leaf of *P. grandidentata* Michx. for comparison of venation with that of *P. washoensis*. Fig. 4. Capsule of *Populus eotremuloides* Knowlt. Fig. 5. *Populus dolichophylla* n. sp. Fig. 7. *Salix venosiuscula* n. sp. Type no. 21464 U. M. Fig. 8. *Salix Fendleriana* Anders. from Gunnison County, Colo., Univ. of Mich. Herb.

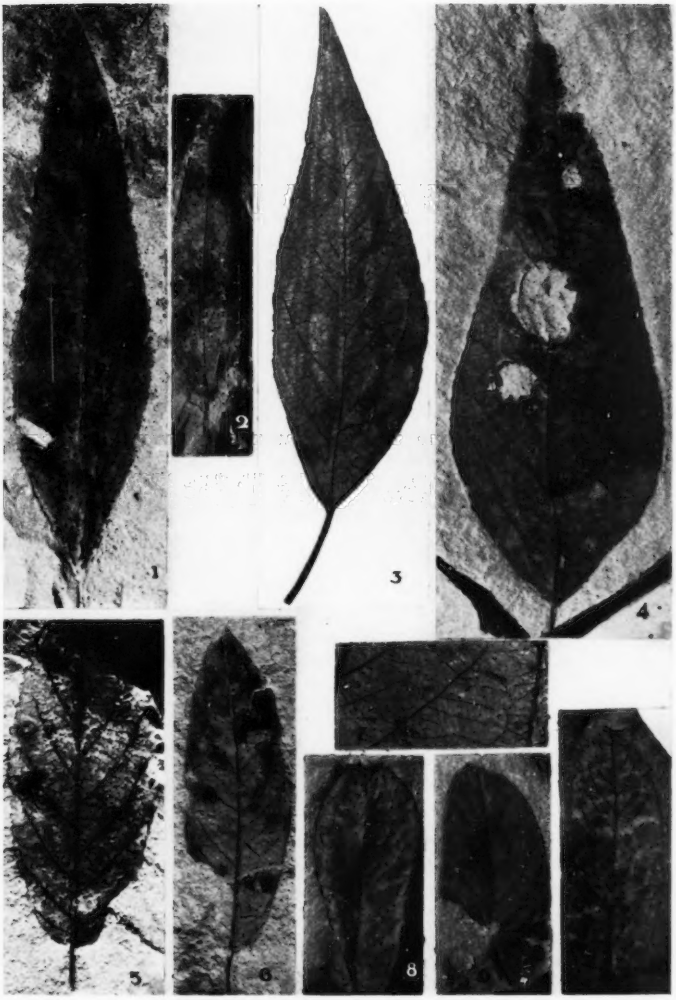
(Plate 4, fig. 3), the narrow-leaf cotton wood, has essentially the same type of leaves and is abundant along Thorn Creek. It, like the fossil species, is characterised by the cuneate base, the small crenate teeth which are absent only from the basal region, the long ovate-lanceolate shape and secondaries that in the main part of the blade are essentially equal in strength. *P. angustifolia* grows along the banks of streams usually at fairly high altitudes and is the common cottonwood of the Rocky Mountain states. The fossil leaves also show some resemblance to *P. acuminata* Rydb., the lance-leaved cottonwood found along streams in the dry foothill region of the eastern side of the Rocky Mountains from Alberta to western New Mexico. This species has leaves that are relatively broader and shorter and have more prominent teeth than the Thorn Creek fossils.

Populus eotremuloides Knowlt. Plate 3, fig. 4; plate 4, fig. 7. Knowlton described this species from beds of the Payette formation southeast of the old Marsh (Montour) post office, Gem County, Idaho. It has since been reported from a number of western Miocene localities.

As has been previously suggested, it resembles the cottonwoods *P. balsamifera* L. and *P. trichocarpa* T. & G. The scanty Sucker Creek material in my collection was considered to be very much like the former (33), whereas the Thorn Creek leaves are clearly more like *P. trichocarpa*. These fossils exhibit a considerable variation, but the character of the fine venation and the regular spacing of the secondaries is constant throughout. The major variation occurs in shape, which may be rhombic-lanceolate to broadly ovate or even slightly cordate. This change in shape is, of course, matched by a variation in the base from narrowly cuneate to cordate. There is indication of a difference in texture, the narrow leaves being apparently very thin and having a distinct, fine venation; the broad ones appearing to be subcoriaceous with fairly obscure venation. While this range of variation is somemhat greater than that indicated by the illustrations of the species in some recent publications, it is no greater than that indicated in the poplar leaves of the cottonwood type described by Knowlton from the Payette formation. Neither is it any greater than the variation which I observed on a single tree of *P. trichocarpa* at Lake Crescent, Clallam County, Washington. This cottonwood is found in the Coast Ranges from Alaska to southern California and is said to be the commonest tree along the streams of the Continental Divide in Idaho and Montana.

Populus washoensis Brown. Plate 3, fig. 1, 2, 6. Recent collections have increased the number of specimens of this species considerably. They show much more variation than the few original impressions. The teeth on one leaf are somewhat small and quite curved, but the shape and venation are typical. Two specimens are very much like some of the smaller leaves described and illustrated as *P. heteromorpha* Knowlt. (23) and since transferred to *Cebatha*. These leaves are almost identical with certain leaves of *P. alba* L. and P. *canescens* Smith. The majority of the leaves find their greatest similarity among living species with *P. grandidentata* Michx. (Plate 3, fig. 3), the large-toothed aspen of the eastern United States. The small leaves are probably merely variants.

PLATE 4



Figs. 1, 2, 4. *Populus dolichophylla* n. sp. Fig. 4 type, no. 21459 U. M. Fig. 3. *Populus angustifolia* James from Winnemucca, Nev., in Univ. of Mich. Herb. Fig. 5. *Alnus corrallina* Lesq. Fig. 6. *Salix venosiuscula* n. sp. Fig. 7. Detail of venation of *Populus eotremuloides* Knowlt. Fig. 8. *Salix boisiensis* n. sp. Figs. 9, 10, *Salix spokanensis* (Berry) Brown.

Salix boisiensis n. sp. Plate 2, fig. 3; plate 4, fig. 8. Leaves oblong-obovate, 3.2-3.8 cm. long, 1.7 cm. broad; apex rounded; base unevenly cuneate; margin entire; midrib stout, prominent to the apex; prominent secondaries about 12 pairs, often with an additional single intermediate vein between adjacent major secondaries, secondaries arising from the midrib at angles of 70-75° near the base, 55-70° near the middle of the blade and 30 40° at the apex; tertiaries forming an irregular coarse reticulum; petiole 7 mm. or more in length, curved on the only specimen in which it is preserved; texture thin but firm. Type no. 21466 U. M.

These leaves may be matched with surprising exactness by leaves of *S. delnortensis* Schneider (specimens from Smith River, Calif., in the University of Michigan Herbarium). They are also almost equally like *S. Scouleriana* Barr., the black willow, found growing along Thorn Creek. Its range extends from Alaska to northern California and to the eastern ranges of the Rocky Mountains.

The fossils are also very similar to variants of a number of species of *Salix*. Such variants are decidedly in the minority and are not satisfactory for comparison with fossils unless the range of variation exhibited by the living species is also encountered in the fossils. Such is not the case in the willow leaves from the Thorn Creek bed. Leaves of none of the other three recognised fossil species resemble the normal leaves of those species in which a few varying leaves seem to be similar to *S. boisiensis*.

The problem of the best disposition to be made of species of *Salix* is a complex one. It, like the study of fossil leaves of *Quercus*, is complicated by the unsatisfactory diagnosis of species by leaf characters alone, and by the disagreement among taxonomists as to the identification of species. At the risk of indicating too many species, I feel that it best to recognise four species of *Salix* in the Thorn Creek collection since this seems to give the most exact picture of the diversity of willows encountered. In a modern flora so many leaf forms would indicate several different types even if some intermediates were present.

Salix Schimperi Lesq. Plate 5, fig. 1. Leaves of this species are among the most numerous in the collection. Because of the length of the leaves and the prevalent checking and breaking of the matrix there are no perfect specimens. They bear a close resemblance to the common heart-leaved willow, *S. cordata* Muhl. (Plate 5, fig. 2).

Salix spokanensis (Berry) Brown. Plate 4, figs. 9, 10. There are several easily recognisable leaves of this species. They are remarkably uniform in shape and size, the smallest is 1.3 by 2.9 cm. and the largest 1.3 by 3.4 cm. Berry (5) described the species as *Rhamnus* from the Latah at Spokane, Washington and the Thorn Creek specimens appear to be almost identical with his figures. A careful study of the available herbarium material did not show any species of *Rhamnus* with consistently small leaves. However, there is an undeniable resemblance to certain small leaves of *R. cathartica* L., the european buckthorn.

Brown (10, p. 168) transferred this species to *Salix*. I feel that the reasons for this transfer are not much better than the reasons for retaining it in *Rham-*

PLATE 5

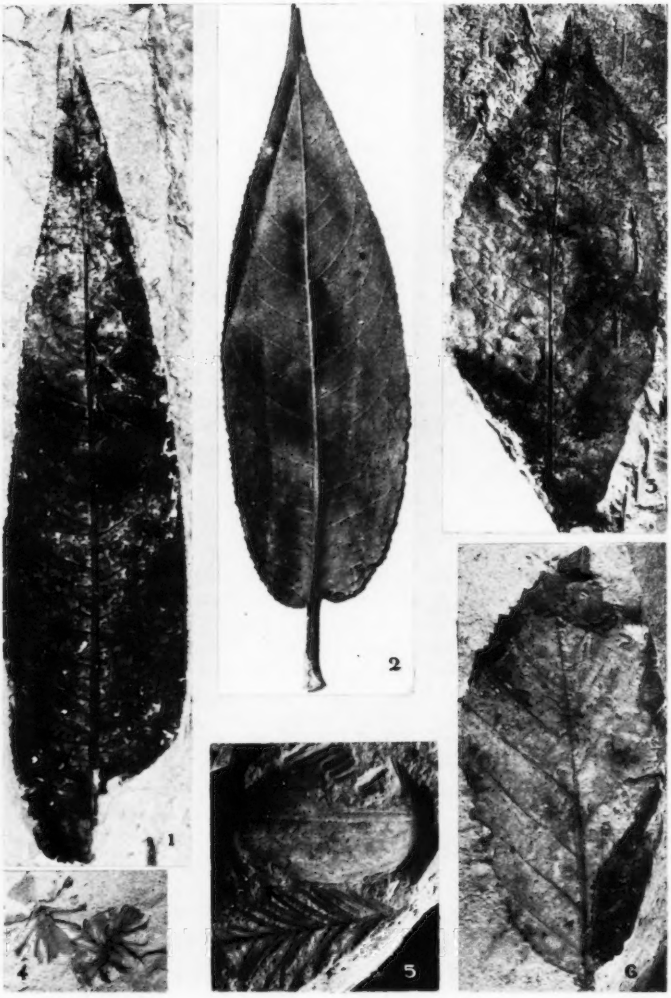


Fig. 1. *Salix Schimperi* Lesq. ×3/4. Fig. 2. *Salix cordata* Muhl. from Watersmeet, Mich., in Herb., Univ. of Mich. Fig. 3. *Carya egregia* (Lesq.) LaMotte. Fig. 4. *Alnus* sp. cones. Fig. 5. *Carya pecanoides* (Chaney) n. comb. Fig. 6. *Alnus corrallina* Lesq.

nus, but am, nevertheless, following his change.It is probable that this species does not belong in either genus and it may really belong, as Brown suggested, in *Lonicera.* His figure of *Salix commutata denudata* Bebb. does show venation essentially like that of the fossil, but it does not, and neither to the herbarium specimens available to me, give any indication of the basal teeth said to be on the Latah specimens.

S. commutata var. *denudata* is a plant of alpine and subalpine bogs and there is little likelihood that it is really the nearest of kin to the Thorn Creek specimens even if they are correctly placed in Salix.

Salix venosiuscula n. sp. Plate 3, fig. 7; plate 4, fig. 6. Leaves membranaceous, narrow elliptic or very slightly obovate, rather small, 5.8 cm. long, 1.3-1.6 cm. wide; margin finely and regularly serrate; apex acute; base rounded; secondaries distinct but slender, irregular in spacing, about 13-15 pairs, arising at an angle of about 40° and curving upward near the margin; intermediates few; finer venation a coarse, irregular, rather prominent reticulum; petiole stout, at least 1 cm. long. Type no. 21464 U. M.

The living *S. Fendleriana* Anders (Plate 3, fig. 8) has leaves that are quite similar. This is a small shrub or tree of the submontane and montane zones. It is common in the Rocky Mountains of the United States. *S. lasiandra* Benth. also has leaves similar to the fossil and is often considered to include *S. Fendleriana* as a variety, or even as an inseparable phase.

Juglandanceae

Carya egregia (Lesq.) LaMotte. Plate 5, fig. 3. The two fragmentary leaflets are smaller and more delicate in appearance than those LaMotte (24) illustrated from the Upper Cedarville formation, but are similar in the essential characters of shape and venation.

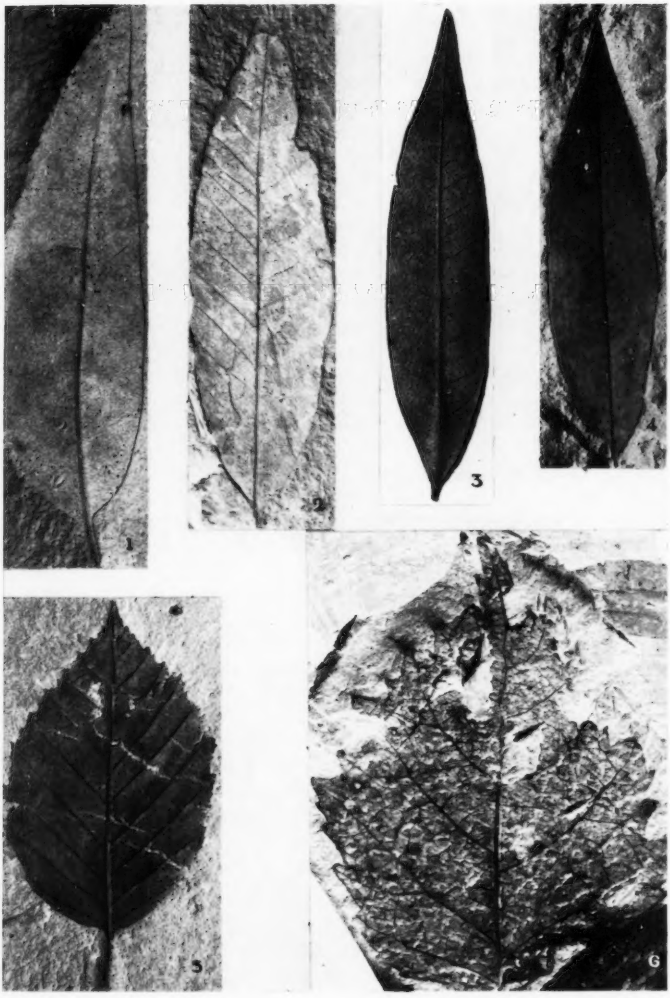
I have not felt justified in associating these leaflets with the pecan fruit treated below because pecan leaflets in the living types are distinctive by their narrow and somewhat falcate form. At isolated localities for typical hickory in Mexico a pecan grows in the same habitat. Likewise, pecans and hickories are such common associates in the United States that it is not necessary to consider the leaflets and the nut in the Thorn Creek bed as necessarily conspecific. If both were so scarce as to leave a numerically almost negligible record in the deposit, it might easily be that one would be represented only by foliage and the other by fruit.

Carya pecanoides (Chaney) n. comb. Plate 5, fig. 5. A species of pecan was described as *Hicoria pecanoides* from the Eagle Creek flora. Although this Thorn Creek specimen may not represent the same species it is referred to it as I feel that there are no sufficiently definite distinguishing characters for fossils of this type.

Betulaceae

Carpinus payettensis n. sp. Plate 7, fig. 4. Involucre leaf-like, 3-lobed, the main lobe much longer than the lateral ones; main lobe with 3 coarse teeth on each side, upper pair opposite, very long and narrow, each tooth entered

PLATE 6



Figs 1, 2, 4. *Castanopsis angustifolia* n. sp. Fig. 4. Type, no. 21474 U. M. Fig. 3. *Castanopsis chrysophylla* (Hook.) DC. from Hood River, Ore., in Herb., Univ. of Mich. Fig. 5. *Alnus carpinoides* Lesq. Fig. 6. *Betula lacustris* MacG.

by a distinct vein from the midrib from point of attachment of involucre; lateral lobes apparently not over 1.2 cm., middle lobe 2.6 cm. (estimated). Type no. 21470 U. M.

A single specimen and its counterpart appear to represent an involucre of *Carpinus*. Although the nut is lacking there can be little doubt as to the correctness of this identification. Both the coarse and fine venation have exactly the same aspect as the venation of the involucres of *Carpinus caroliniana* Walt. (Plate 7, fig. 3), the common eastern blue beech or hornbeam. The strong marginal teeth and the stout veins entering the lower lobes and teeth directly from the point of attachment are also suggestive of that species. On the other hand, the rather narrow and quite elongate middle lobe is more suggestive of *C. Betulus* L. It is unfortunate and rather surprising that no leaves of *Carpinus* have been recognized in this collection.

Betula lacustris MacG. Plate 6, fig. 6. The Thorn Creek specimens are very similar to the figured type of this species from Trout Creek (28). The leaves are characterized by being ovate, membranaceous and coarsely serrate except at the base. *B. papyrifera* var. *occidentalis* is somewhat similar but *B. fontinalis* is probably the nearest ally. The latter grows along stream banks throughout the mountain areas of the West. At Thorn Creek it is abundant as a low shrub-like tree.

Alnus carpinoides Lesq. Plate 6, fig. 5. This extremely abundant and variable Miocene alder is represented in the Thorn Creek collection by only a few specimens. These are quite similar to the leaves of *A. sinuata* (Regel) Rydb. which is found from Alaska through the Coast Ranges and Rocky Mountains.

Alnus corrallina Lesq. Plate 4, fig. 5; plate 5, fig. 6. This common Miocene *Alnus*, rare, like the preceding, at Thorn Creek, appears to be most like the living *A. rhombifolia* Nutt. and *A. rugosa* K. Koch. Certain specimens of the latter are very similar to the fossil except for their greater width and tendency toward obovateness. Aments probably similar to this living species have also been found. On the whole, *A. rhombifolia* seems to come the nearest to duplicating the Miocene species. This white alder grows in northern Idaho and extends to the eastern slope of the Cascade Mountains in Washington and Oregon. In California it is found in the major mountain chains.

Alnus sp. Aments. Plate 5, fig. 4. Aments apparently similar to those of *A. rugosa* are included in the collection but are not assigned to either of the two leaf species of *Alnus*.

Fagaceae

Fagus pacifica Chaney. Plate 11, fig. 5 (*F. washoensis* LaMotte, Carnegie Inst. Wash. Pub. 455:119, pl. 8, figs. 2, 3, 5. 1936. *Castanea Lesquereuxi* LaMotte, Carnegie Inst. Wash. Pub. 455:130, pl. 9, figs. 4, 5. 1936.)

Since my preliminary report (34) on this flora was written further studies have been made of the variation to be found in the living American species of *Fagus*. Also more fossils have been collected. These studies have confirmed my previous suggestion that there is some doubt whether two species of beech have been found in the western Miocene. With the series of fossil and com-

PLATE 7

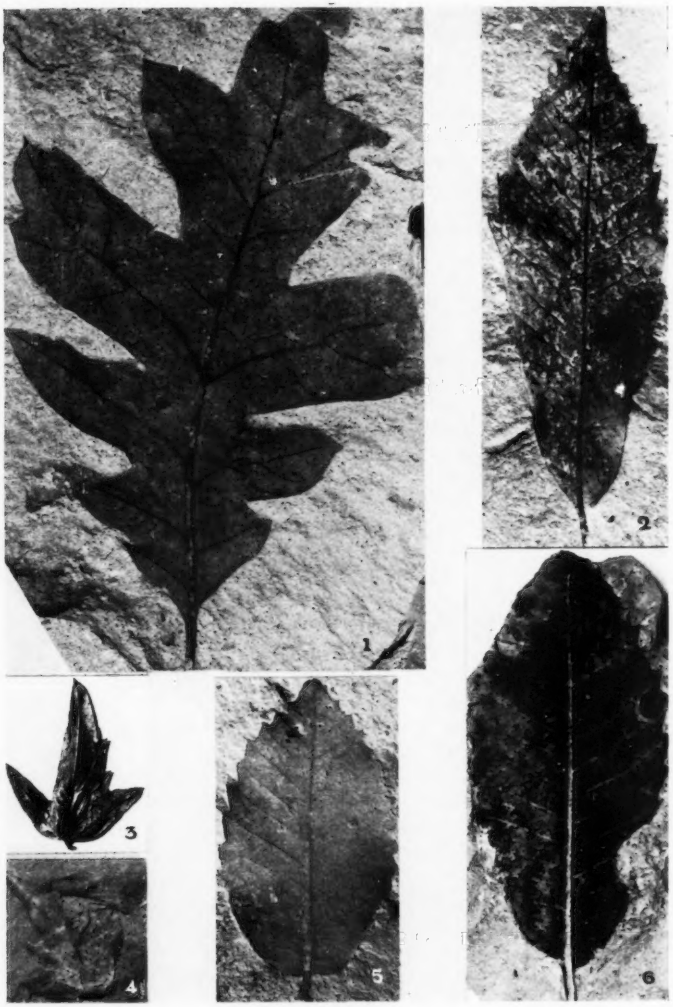


Fig. 1. *Quercus pseudolyrata* Lesq. Figs. 2, 6. *Quercus clarnensis* Chaney. Fig. 3. *Carpinus caroliniana* Walt. (bract) from Washtenaw Co., Mich. in Herb., Univ. of Mich. Fig. 4. *Carpinus payettensis* n. sp. No. 21470, U. M. Fig. 5. *Quercus Brownii* Brooks.

parable living leaves now at hand, I do not believe that *F. washoensis* can be maintained as distinct from *F. pacifica*. In fact, I would even go so far as to suggest that all the western Miocene leaves referred to *Fagus* should be referred to a single species. If this were done the name would have to be *F. sanctieugeniensis* Hollick on the basis of priority.

F. pacifica was described from material collected on Gray's ranch in the Crooked River Basin, Oregon. As only seven leaf impressions were included in that collection the complete range of variation was not evident. Two of the three figured leaves are, according to the evidence from Thorn Creek, not to be regarded as really typical of the species. They can, however, as Chaney (14) pointed out, be duplicated by some leaves of the living *F. grandifolia* Ehrh. Living counterparts, for instance, were collected by the writer in the Great Smoky Mountains of Tennessee. About a half dozen similar leaves have been noted in the Thorn Creek collection, among much more numerous leaves of a more typical form.

F. washoensis was based on collections from 49 Camp, Nevada and Pit River, California. LaMotte compared his specimens with the Asiatic beech, *F. longipetiolata* Seeman. No specimens of that species are available to the present author, but the figures given by LaMotte (24) for comparison differ strikingly in marginal characters from the fossil material which he illustrates. In the living species the margin dips in at the ends of the secondaries forming an undulate margin, in the fossils, both as described and illustrated, the margin is dentate or serrate with triangular teeth terminating the secondaries. These leaves, to judge from the illustrations, are readily matched by leaves of *F. grandifolia* which I collected in Tennessee.

Several minor differences have been noted between these supposedly distinct fossil species, but to my mind they all break down when a large amount of material is examined. The occurrence in the western Miocene of a single species of *Fagus* of eastern American aspect is quite in keeping with expectation when the relationship of the floras is considered.

F. pacifica was an important constituent of the Miocene forests. It has been reported from the Crooked River Basin, Tipton and Austin, Oregon; the Latah of northern Idaho and eastern Washington; Sucker Creek, Idaho; the Upper Cedarville at 49 Camp, Nevada and Pit River, California. It is very abundant at Thorn Creek where it is second in numerical importance.

The American beech is important in the climax deciduous forest of eastern America.

Castanopsis angustifolia n. sp. Plate 6, figs. 1, 2, 4. Leaves subcoriaceous, narrowly elliptic or lanceolate, up to 6 cm. long, 2 cm. wide, narrowing equally from the widest point about the middle to the acuminate apex and slightly cuneate base; midrib not conspicuous; secondaries weak, closely set, almost parallel, subopposite, about 14-16 pairs, ending near the margin or occasionally bending upward just within the margin; finer venation a fairly fine, mostly quadrangular reticulum with a few weak percurrent tertiaries; margin entire, at times very slightly undulate; petiole stout. Type no. 21474 U. M.

PLATE 8

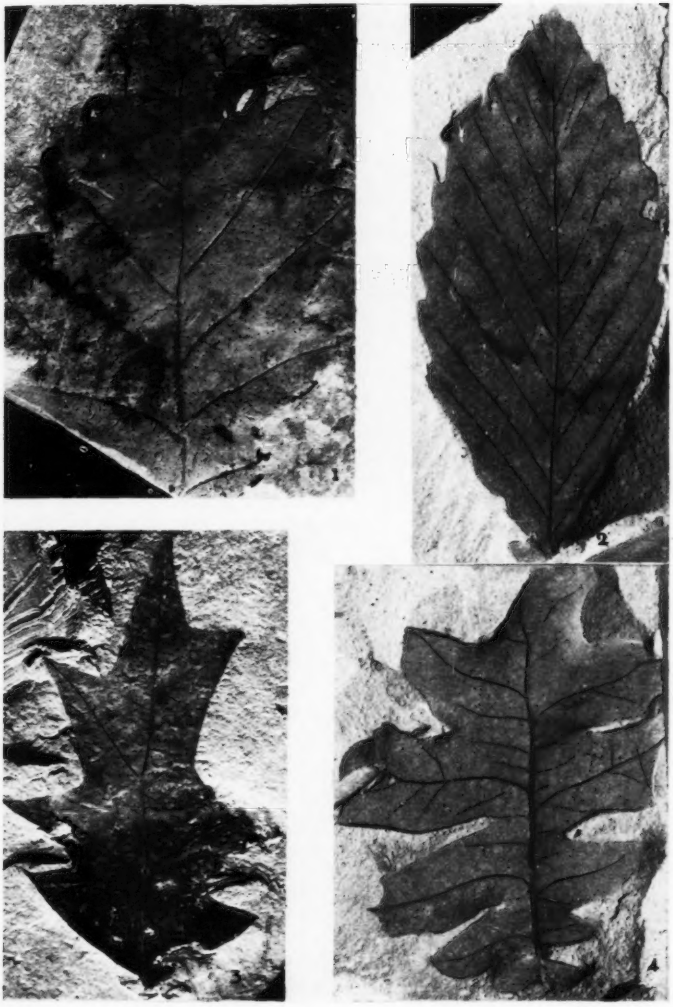


Fig. 1. *Quercus Maccanni* Berry. Fig. 2. *Quercus Eoprinus* Smith. Fig. 3. *Quercus Merriami* Knowlt. Fig. 4. *Quercus deflexiloba* n. sp. Type, no. 21496 U. M.

Three species of *Castanopsis* have been described from the western Miocene. Lesquereux described *C. chrysophylloides* from Chalk Bluffs, Nevada County, California, and Dorf has since reported it from the Pliocene of California. Brooks (9) has transferred certain species previously referred to *Quercus* to this genus as *C. convexa* and *C. consimilis*. Of these three, the first is the most similar to the Thorn Creek specimens, but as illustrated, is, nevertheless, quite distinct in shape and venation.

C. angustifolia leaves are very much like the narrow, linear-lanceolate ones of the living *C. chrysophylla* DC. (Plate 6, fig. 3). *Castanopsis* is a genus that is found mostly in Asia. It is represented in North America by only two species confined to the Pacific Coast.

Quercus pseudolyrata Lesq. Plate 7, fig. 1. This characteristic species of black oak is well represented at Thorn Creek. *Q. Merriami*, which is somewhat similar, differs in having more oblique sinuses, more tapering lobes and scarcely any tendency toward secondary lobing.

The most similar living species is usually considered to be the California black oak, *Q. Kelloggi*, and the nearest eastern equivalent is *Q. velutina*.

Quercus Merriami Knowlt. Plate 8, fig. 3. Recent collections yielded several excellent impressions of this species which I (34) have previously reported.

Quercus deflexiloba n. sp. Plate 8, fig. 4. Leaf thin, broadly elliptic, deeply lobed; sinuses very narrow, ultimately nearly parallel-sided and rounded, extending ½ to ¾ the distance to the midrib, directed almost perpendicularly to the midrib; lobes 4 or 5 on a side, scarcely tapering, sharp-pointed or broadly tridentate, the central tooth longer than the others and separated from them by a broad, shallow, rounded sinus; principal secondaries with a sigmoid flexure terminating in the apices of the lobes, arising at an acute angle, immediately bending outward and again inward to enter the lobes; intermediate secondaries 2-3 between principal ones, usually weak, soon obscure, but a few giving off weak branches; principal secondaries giving off numerous pinnate veins which may extend to the margin of the lobes; finer venation irregular; base and apex imperfect. Type no. 21596 U. M.

Although this is obviously an oak no living species so far studied has the same combination of characters. *Q. Catesbaei* does, in some specimens, have the same type of tridentate lobes. Since the fossil is unlike any of the other fossils it is considered to be a different species even though it is possible that it may represent merely a variation of another type.

Quercus simulata Knowlton. Plate 9, fig. 7. Small leaves of the general type of this species are abundant in many western Miocene beds and opinions about their relationships are varied. *Q. hypoleuca* Engelm. from the southwest and northern Mexico appears to be the nearest living equivalent among American oaks.

Quercus clarnensis Trel. Plate 7, figs. 2, 6; plate 9, fig. 3; plate 11, fig. 4.

PLATE 9

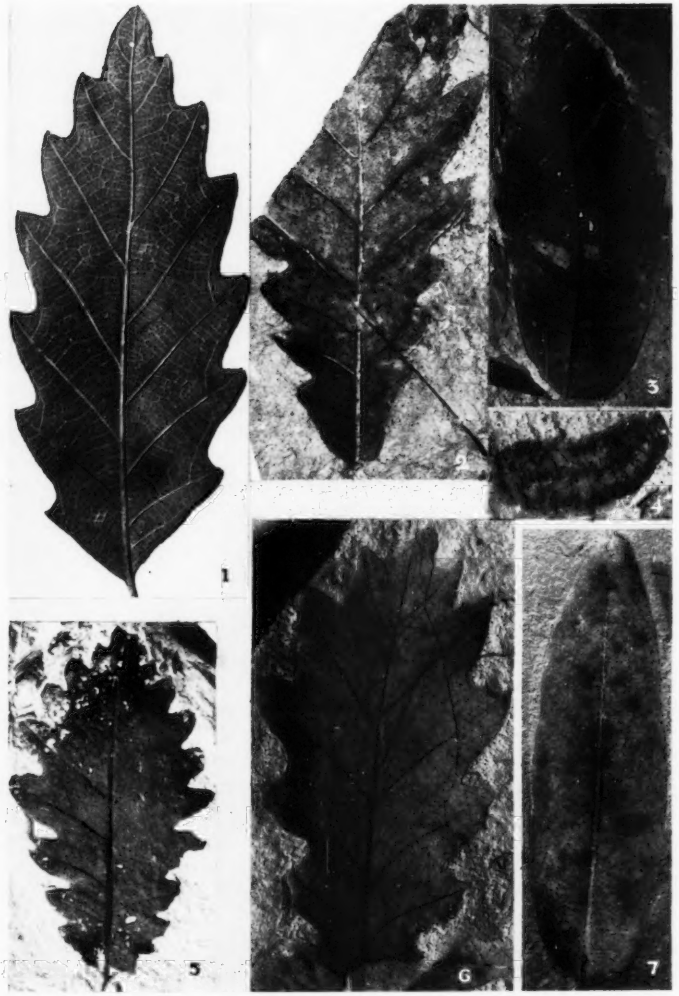


Fig. 1. *Quercus Muehlenbergii* Engelm. var. *Brayi* Sarg. from Guadalupe Peak. Texas, in Herb., Univ. of Mich. Figs. 2, 6. *Quercus payettensis* Knowlt. Fig. 3. *Quercus clarnensis* Chaney. Fig. 4. Staminate catkin? Fig. 5. *Quercus Bretzi* Chaney. Fig. 7. *Quercus simulata* Knowlt.

This is the most abundant species in the Bridge Creek flora of the Crooked River Basin of Oregon and Chaney has also reported it from the Payette formation. It is well represented at Thorn Creek. The leaf impressions from Thorn Creek exhibit a wide range in variation and were at first considered to belong to two species. However, when a series was studied no constant differences between two "species" could be detected and the leaves are all grouped as *Q. clarnensis*. As illustrated and described by Chaney (14) the Bridge Creek specimens have as great a range of variation as these from Idaho. No closely related living species has been suggested.

Quercus Browni Brooks. Plate 7, fig. 5. A few leaves relatively shorter and broader than those above may be assigned to *Q. Browni*. The teeth are blunter than those on the leaves from Sucker Creek. Leaves of this species are seldom more than 2½ times as long as they are broad. The nearest living equivalent seems to be *Q. chrysolepis* Leibm., a live oak of the California Coast Ranges.

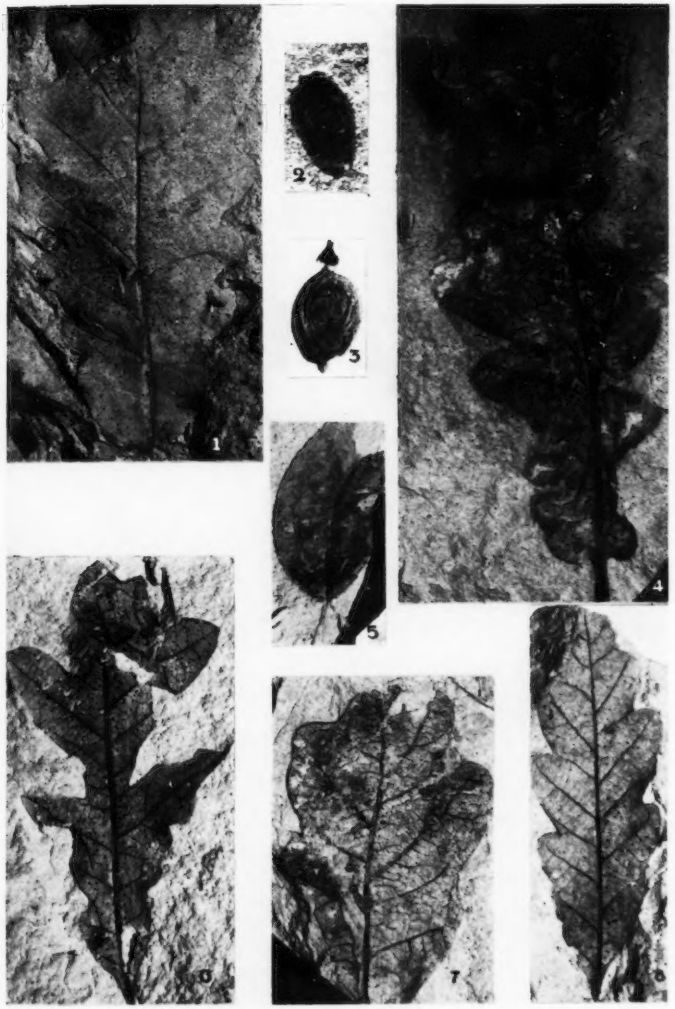
Quercus Tuckeri n. sp. Plate 10, figs. 6-8. Leaves firm, narrowly elliptic or slightly obovate, 5-5.5 cm. long, 1.5-2.7 cm. wide, lobed; base narrowly cuneate; apex acute to obtusely rounded; margin shallowly round-lobed, lobes 2-4 (generally 3 or 4) pairs, usually approximately equal in size; sinuses shallow, angled or abruptly rounded, usually directed downwardly; midrib moderately stout; secondaries 9-10 pairs, those terminating in the ends of the lobes usually a little stronger than the others, the one or two pairs of intermediate secondaries between the lobes go to or just above the sinuses, those arising in the upper part of the blade above the lobes arch to form loops; tertiaries thin, leaving the secondaries at right angles, percurrent between the secondaries or in the lobes often forming loops with adjacent tertiaries just within the margin. Type no. 21480 U. M.

Q. Tuckeri is readily distinguishable from *Q. payettensis* Knowlton by its rounded lobes, the intermediate secondaries and the presence of distinct tertiaries. *Q. columbiana* Chaney from Eagle Creek and the Latah of northern Idaho is larger, has more lobes and a somewhat different type of venation. Chaney's figure 2, plate 13 (12) appears to be a leaf of the type here included as *Q. payettensis*.

Among living species the shin oak, *Q. breviloba* (Torr.) Sarg., has many of the same characteristics. The venation and form of the lobes of the fossil (but not the shape of the leaf) are strikingly like those of var. *argentata* figured by Trelease (37, Pl. 170). The species is characterized by the elliptic-oblanceolate to obovate-undulate or shallowly round-lobed leaves. It grows in the eastern Sierra Madre region of Mexico and in Texas.

Quercus boisiensis n. sp. Plate 10, figs. 1, 4. Leaves thin, length unknown, the largest preserved for 7.3 cm. which appears to be a little over half the normal length, 3.3 cm. wide; apparently narrowly obovate or narrowly elliptic in shape, lobed; lobes rounded, almost at right angles to the midrib, sinuses shallow, rather narrow; midrib broad, secondaries more than 10 pairs, arising at angles of 55 to 60°, those terminating in the lobes slightly stronger than

PLATE 10



Figs. 1, 4. *Quercus boisiensis* n. sp. Fig. 1 type, no. 21484 U. M. Fig. 2. *Ulmus paucidentata* Smith. Fig. 3. *U. racemosa* Thomas from St. Clair Co., Mich., in Herb., Univ. of Mich. Fig. 5. *Ceanothus* sp. Figs. 6-8. *Quercus Tuckeri* n. sp. Fig. 8 type, no. 21480 U. M.

the others; tertiaries fine, often almost parallel; base moderately broad, distantly auricled or subcordate; petiole stout, 5 mm. long. Type no. 21484 U. M.

This species exhibits many features found in two European oaks, *Q. Robur* and *Q. conferta* Kit. The fossils seem to be even more like *Q. Eastwoodii* Rydb. as illustrated by Trelease (37, pl. 162) in which the leaves are obovate, the sinuses nearly closed and the lobes numerous and crenate. This living species is known only from the southern Rocky Mountain region of Utah.

Quercus Bretzi Chaney. Plate 9, fig. 5; plate 11, figs. 1, 2. A number of excellent specimens of this oak were found during the collecting season in 1939 although none had been found before. Chaney (12) described it from Eagle Creek and Brown (11) has since recognized it in the Latah flora from Spokane, Washington.

This species does not seem to have an exact counterpart in the modern flora, but its leaves are somewhat like those of *Q. bicolor* Willd., the swamp chestnut oak of the northeastern states. The lobes of the fossil leaves are fewer in number and correspondingly larger in proportion to the whole leaf than in the eastern analoque. The outline is also more markedly obovate.

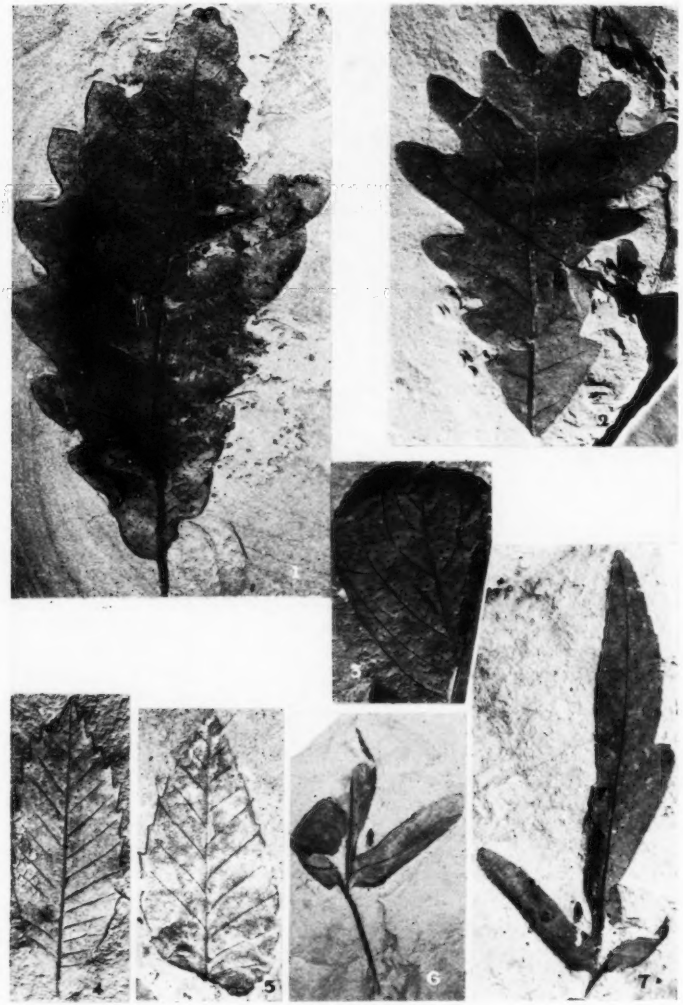
Quercus Maccanni Berry. Plate 8, fig. 1. Since this species has been previously discussed (Smith, 34) no comments are included now.

Quercus Eoprinus Smith. Plate 8, fig. 2; plate 12, fig. 7, plate 14, fig. 7. Additional collections have only served to demonstrate more fully the dominance of this species in the Thorn Creek flora. A few more specimens are illustrated to indicate the variation to be found in the leaves. As I previously suggested the fossils may be readily duplicated by specimens of *Q. montana* Michx. (*Q. Prinus* Auct.) collected in Tennessee.

The leaves of *Q. resinosa* Liebm. from the western Sierra Madre region of Mexico, although much larger, are, as illustrated by Trelease (37, plate 68), strikingly similar and the fine venation is even more like that of the fossils than is that of *Q. montana*. Unfortunately no herbarium material is available for more accurate comparison. Both of the living species mentioned have larger leaves than the fossil and this is particularly true for the Mexican species, a point in favor of regarding *Q. montana* as the closest ally of *Q. Eoprinus*.

Quercus payettensis Knowlt. Plate 9, figs. 2, 6. Leaves thin, firm, narrowly elliptic to obovate, up to 7 cm. long and 3.2 cm. wide, lobed; lobes 3-7 or more pairs, subopposite or alternate, simple, triangular or slightly oblique, rather sharply pointed at apex but apparently not bristle tipped; sinuses shallow, rounded, extending no further than one-third the distance to the midrib; base narrow to round cuneate; apex acute; midrib moderately stout below, straight or slightly curved; secondaries as many as there are lobes, each entering a lobe and terminating in its apex, subopposite, never forking, arising at angles of 18 to 35°; no visible tertiaries; ultimate venation often well preserved, forming a rather fine, regularly quadrangular reticulum.

PLATE 11



Figs. 1, 2. *Quercus Bretzi* Chaney. Fig. 3. *Rhamnus* sp. Fig. 4. *Quercus clarnensis* Chaney. Fig. 5. *Fagus pacifica* Chaney. Figs. 6, 7. *Pyrus heteromorpha* n. sp.

The principal characteristics of this species are the lanceolate or narrow obovate shape, the prominent small lobes and the entire absence of subordinate lobing. *Q. payettensis* was described from Jackass Creek, Boise County, Idaho, by Knowlton. He later recognized it in the Latah of northern Idaho. Because of the large amount of material available and the differences in interpretation of the species by various authors, a description based upon the Thorn Creek material identified as *Q. payettensis* is given above.

The distinction between certain specimens of this species and *Q. Merriami* is somewhat obscure. *Q. payettensis* is usually smaller, more lanceolate or obovate, with distinct deltoid lobes quite regularly spaced. In *Q. Merriami* the lobes are elongated, not so regularly spaced and the sinuses are considerably deeper and more oblique.

Q. payettensis is somewhat like *Q. infralutea* Trel. (Trelease 37, pl. 136) except that in the fossil the teeth are more prominent. This living species is known from the western Sierra Madre region of Mexico. According to Berry (8) the leaves of *Q. payettensis* from fossil localities in northern Idaho resemble those of *Q. Duraznillo pinetorum* Trel. from Mexico. The narrower leaves from Thorn Creek are almost like the northern Idaho fossils and differ from the Mexican species in that the secondaries extend clear to the ends of the simple lobes. The majority of the Thorn Creek specimens are obovate and have broader, more forwardly pointing teeth. The larger leaves resemble those of *Q. Brayi* Small which is often considered to be a variety of *Q. Muehlenbergii* Engelm. This variety of the chestnut oak grows in the southwestern and adjacent Rocky Mountain region of Texas and New Mexico. There is also marked resemblance between the narrower fossil leaves and the living *Q. lancifolia* Chamisso & Schlechtendal as figured by Trelease (37, pl. 32) except that this Mexican species has the leaves toothed only in the upper half. In spite of all these resemblances the fossils probably find their closest affinity with the American species, *Q. Muehlenbergii* (Plate 9, fig. 1). This chestnut oak is a common constituent of the deciduous climax forest of the eastern United States.

Ulmaceae

Ulmus paucidentata Smith. Plate 10, fig. 2; pl. 13, figs. 4, 9. Additional collections yielded a number of excellent specimens of this species. They serve principally to indicate that the elliptic shape is more common than the elliptic-ovate. The doubly or triply serrate nature of the margin is much more noticeable than in the type specimen. All the leaf impressions are decidedly unequal at the base, and in two impressions the base on one side is rounded instead of cuneate as is usual.

The winged seeds, suggestive of those of *U. racemosa* Thomas (Plate 10, fig. 3), may represent the seeds of this fossil species.

Magnoliaceae

Magnolia oregoniana Chaney. Plate 14, fig. 5. No additional specimens were obtained in recent collections so the species is, unfortunately, still poorly

PLATE 12

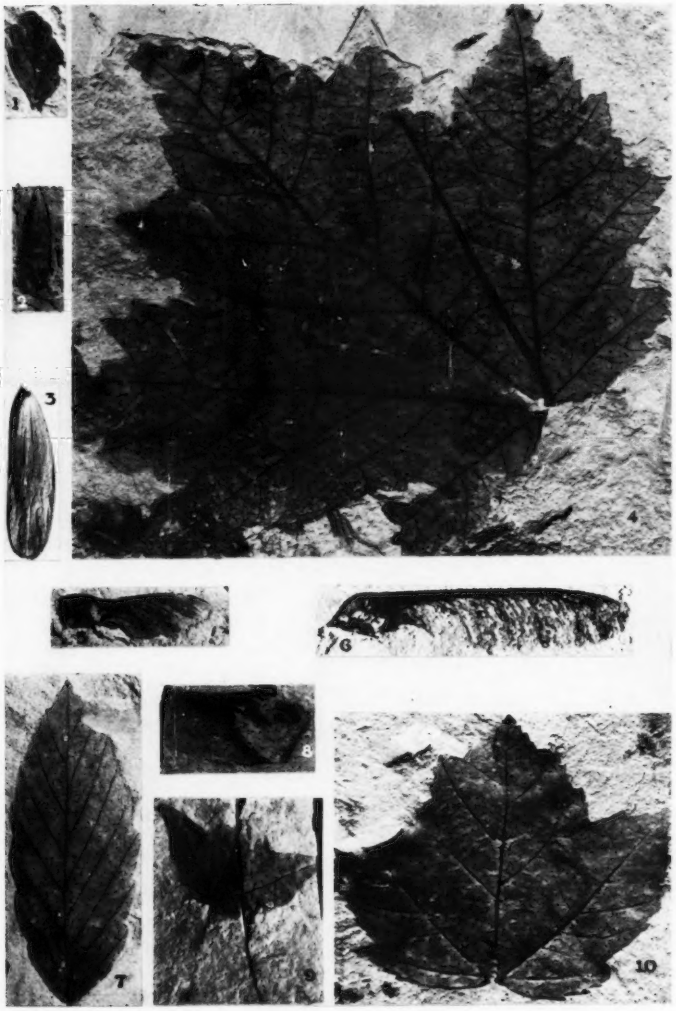


Fig. 1. *Cercocarpus cuneatus* Dorf. Fig. 2. *Fraxinus leptocarya* n. sp. Fig. 3. *F. quadrangulata* Michx. from Allentown, Mo., in Herb., Univ. of Mich. Figs. 4, 10. *Acer glabroides* Brown. Fig. 5. *Acer* sp. samara. Fig. 6. *Acer* sp. samara. Fig. 7. *Quercus Eoprinus* Smith. Figs. 8, 9. *Acer Scottiae* MacG.

represented in the Thorn Creek flora. The single specimen resembles *M. virginiana L.*

Rosaceae

Amelanchier dignata (Knowlt.) Brown. Plate 13, fig. 2. A single small leaf is referred to this species. It differs from most of the illustrated specimens in its smaller size, in the greater irregularity of the secondaries and in having teeth well below the middle of the blade.

Amelanchier subserrata n. sp. Plate 13, fig. 1. Leaves thin, orbicular or slightly longer than broad, 1.3-3 cm. wide, 1.8-3.5 cm. long; broadly obtuse above, but apex minutely short-acuminate by the small tooth at the end of the midrib; base broadly rounded; margin entire along the lower half, toothed above, teeth obtuse, pointing toward the apex; midrib stout, straight; secondaries 5-10 pairs, thin, forming a broad angle with the midrib, curving upward and entering the teeth or forking once to send branches to two teeth; secondaries in lower part of blade becoming extinct along the margin; tertiaries percurrent, almost perpendicular to the midrib; ultimate venation a very fine reticulum; petiole preserved for a distance of 2.2 cm. Type no. 21506 U. M.

The ovate-orbicular shape serves to distinguish this *Amelanchier* from the other western Tertiary species. Among living species, *A. elliptica* A. Nels. (Plate 13, fig. 7) has esesntially the same characters as to shape, size and margin. The chief difference lies in the more acute angle at which the secondaries of the living species arise and in its more conspicuous coarse teeth. *A. elliptica* is a small, slender, tree-like shrub that usually grows scattered in wet open places in the mountains of Colorado, Wyoming and Utah.

A. serrata differs from *A. dignata* in its shorter teeth, more definite tertiary venation and more nearly round leaf shape. It is possible that a good series of specimens would show an intergradation between these two and would indicate that they belong to the same species.

Cercocarpus cuneatus Dorf. Plate 12, fig. 1. Dorf described this species from the Pliocene of California and Axelrod recognized it in the Mt. Eden beds. The Thorn Creek leaves are somewhat narrower and appear to have been more coriaceous than those previously figured.

The living mountain mahogany, *C. montanus* Raf. (*C. parvifolia* Nutt.) is quite similar to the fossil. *Cercocarpus* is a North American genus confined to the dry interior and mountainous regions and to Santa Catalina Island. Two species are known to occur in the northern Rocky Mountains and the mountain mahogany is very common on the low hills of southwestern Idaho. It often forms the most conspicuous plant over considerable areas. It was not observed in the immediate vicinity of Thorn Creek but in all probability it does occur in the Boise Mountains.

Crataegus microcarpifolia Arnold. Two small leaves, the most complete of which is 3 cm. wide and 3.5 cm. long (estimated) appear to be indistinguishable, except in size, from *C. microcarpifolia* as illustrated by Arnold (3) from Trout Creek. These impressions are very similar to forms that have been

PLATE 13

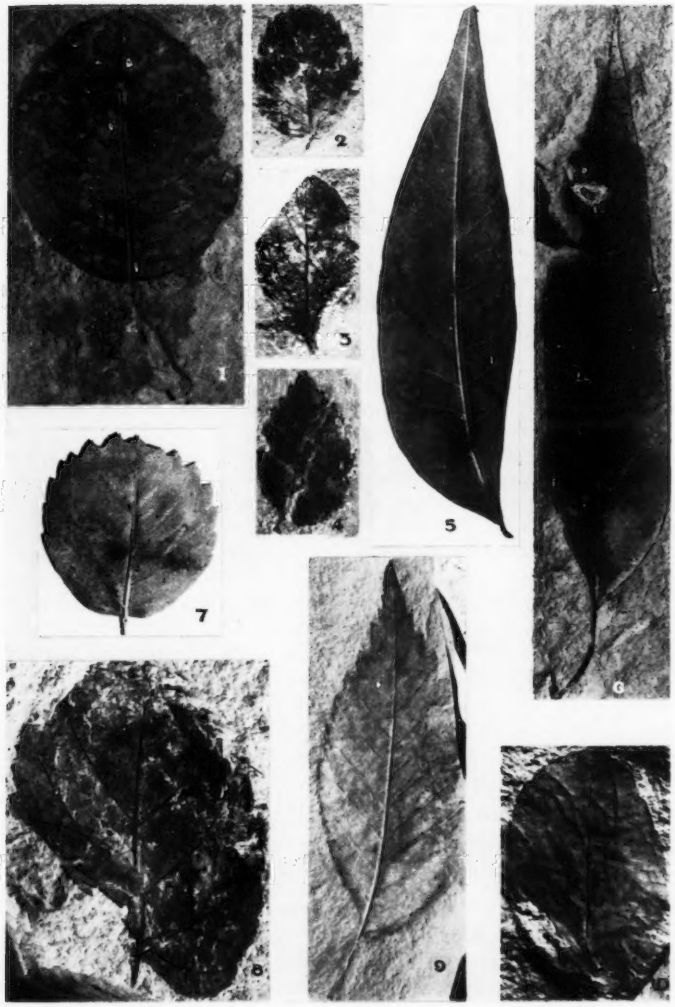


Fig. 1. *Amelanchier subserrata* n. sp. Type, no. 21505 U. M. Fig. 2. *Amelanchier dignata* (Knowlt.) Brown. Fig. 3. *Symphoricarpos elegans* (Lesq.) Smith. Figs. 4, 9. *Ulmus paucidentata* Smith. Fig. 5. *Sapindus Drummondii* Hook. & Arn. from Rio Grande, Hidalgo Co., Texas, in Herb., Univ. of Mich. Fig. 6. *Sapindus idahoensis* n. sp. Type, no. 21517 U. M. Fig. 7. *Amelanchier elliptica* Nels. from Medicine Bow Nati. Forest, Wyo., in Herb., Univ. of Mich. Fig. 8. *Tilia parvulifolia* n. sp. Type, no. 21518 U. M. Fig. 10. *Prunus covea* Chaney.

referred to *C. Newberryi* Cockerell and may be indistinguishable from it. With the taxonomic confusion of living *Crataegus* a paleobotanist can hardly hope to do more than place fossils in the genus. Any comparison with living species is too unreliable to be worth very much. However, among living species studied, *C. pinnatifida* Bunge, although not an exact counterpart, is somewhat suggestive of these fossil leaves. This living species occurs in eastern Asia.

Prunus Chaneyi Condit. A single specimen is apparently indistinguishable from Condit's figure 3 (15, pl. 5) of *Prunus Chaneyi*. He described the species from material collected at several localities of the San Pablo formation of California. In his estimation *P. serotina* is the closest living ally. I fail to see a resemblance to the fossil in this living species but have no better suggestion on offer.

Prunus covea Chaney. Plate 13, fig. 10. The Thorn Creek fossils included under this name bear a closer resemblance to the figure of the living *P. emarginata* Walp., which Chaney (14, pl. 15, fig. 5) figured for comparison with *P. covea*, than to the illustrated fossils themselves.

Pyrus heteromorpha n. sp. Plate 11, figs. 6, 7; plate 14, fig. 6. Leaves lanceolate or narrowly lanceolate with one or more pairs of long basal lobes, the specimens available with one or at most two pairs of lobes; lowest lobes the largest, each entered by one major secondary near the middle and two minor ones near the margins; apex acute; margin at apex of leaf and of lobes serrate, otherwise entire; texture thin but apparently firm. Type no. 21504 U. M.

These impressions are suggestive of the Asiatic species *P. chinensis* as cultivated at the Michigan Botanical Gardens. They are also slightly similar to some species of *Crataegus*, but it is not possible to find a definite living analoque. The reference to *Pyrus* is made because that genus is more likely to include anomalous types showing the transition from simple to pinnate leaves than is *Crataegus*.

Meliaceae

Cedrela pteriformis (Berry) Brown. Plate 14, fig. 2. It is with considerable doubt that I refer this leaf to *Cedrela*. The reference is made because Brown (10) has so regarded Berry's figure of *Umbellularia dayana* from the Latah the figure of which so closely resembles the Thorn Creek leaf. It does not seem to be in keeping with the generic composition of this flora to find *Cedrela*, and I suspect that too many leaf-types are now being referred to that genus. No seeds identified as *Cedrela* have been found at Thorn Creek.

Aceraceae

Acer glabroides Brown. Plate 12, figs. 4, 10. The name used for this species is that suggested by Brown for those leaf impressions that are most similar to the western *A. glabrum*. Many of these have previously been referred to *A. Osmonti* which is comparable with the living *A. saccharinum* L. *A. Osmonti* in general has deep sinuses and fairly long narrow lobes.

Acer Scottiae MacG. Plate 12, figs. 8, 9. A few small leaves and a broken

PLATE 14

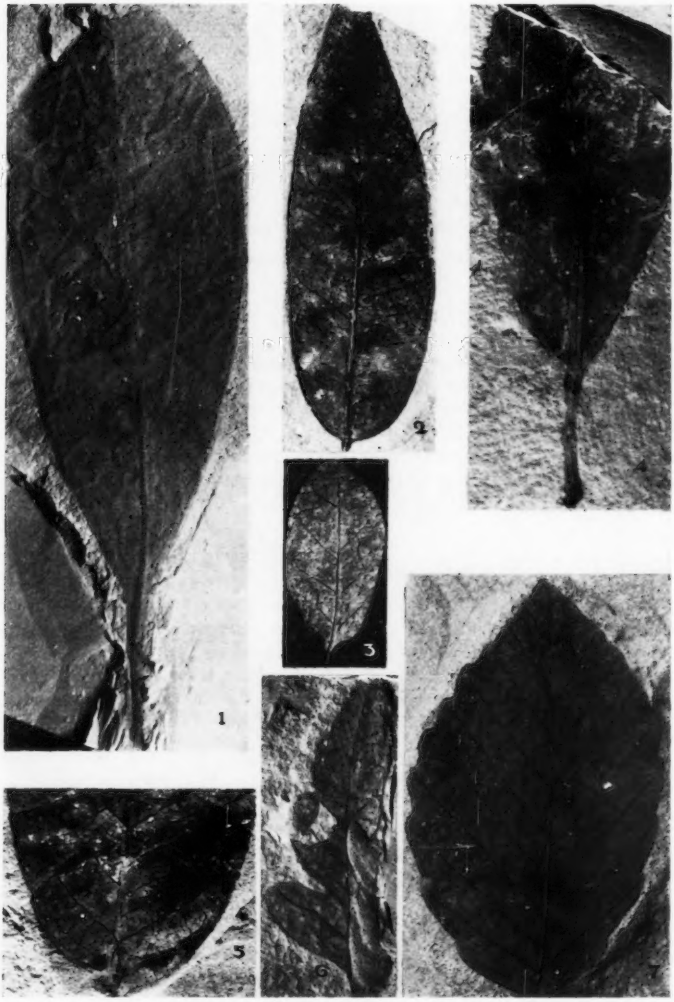


Fig. 1. *Arbutus opaca* n. sp. Type, no. 21519 U. M. Fig. 2. *Cedrela* ? *pteriformis* (Berry) Brown. Fig. 3. *Diospyros elliptica* Knowlt. Fig. 4. *Arbutus idahoensis* (Knowlt.) Brown. Fig. 5. *Magnolia oregoniana* Chaney ×1½. Fig. 6. *Pyrus heteromorpha* n. sp. Fig. 7. *Quercus Eoprinus* Smith.

samara may represent this species although it is hard to explain the absence of any large leaves or fragments of large ones. MacGinitie described this maple from Trout Creek, Oregon, and it has since been reported from the beds at Weiser and south of Horseshoe Bend, Idaho, and from Sucker Creek, Oregon.

The leaves and samaras in this collection are suggestive of those of *A. pictum* Thunb. The samaras also resemble to some extent those of *A. circinatum* Pursh, but the nearest affinity to a living species is probably to one of the Asiatic types. The samaras are much like those of the European *A. campestre*, but this species has distinctive foliage totally unlike any of the fossil impressions.

Acer sp. samara. Plate 12, fig. 6. No living analoque nor closely similar species has as yet been located for this very beautifully preserved samara.

Acer sp. samara. Plate 12, fig. 5. No living analoque has been found for this samara which, like the preceding, is the only one of its kind in the collection.

Sapindaceae

Sapindus idahoensis n. sp. Plate 13, fig. 6. Leaves subcoriaceous, linear lanceolate, up to 9 cm. wide, 1.8 cm. wide, decidedly inequilateral but not falcate; apex long-acuminate; base unequal, narrowly cuneate on one side, slightly rounded on the other; midrib stout, tapering; secondaries thin, about 17 pairs, alternate, the basal ones on the cuneate side arising at angles of about 65° from the midrib; finer venation an obscure, irregular reticulum; margin undulate, slightly thickened; petiole 1.1 cm. long. Type no. 21517 U. M.

Because of the confusion existing between the genera *Sapindus* and *Cedrela* in the western fossil beds it is somewhat difficult to place this type of leaf correctly. A comparison of the living species of these two genera indicated that this fossil species is much more like a *Sapindus* than a *Cedrela* leaflet. Among previously illustrated fossils it is similar to *S. Dentoni* Lesq. and to some of the narrower leaves of *S. oregoniana* (transferred to *Cedrela* by Brown). *S. spokanensis*, reported from the Latah, is about the same shape and size, but judging by the illustrations it is not petiolate. The apparent living analoque for the Thorn Creek leaves is *S. Drummondii* (Plate 13, fig. 5) of the southwestern United States and northern Mexico.

Rhamnaceae

Rhamnus idahoensis Brown. The species was described from the beds at Salmon, Idaho, and since reported from the Latah of Washington. The single specimen is very similar to leaves of *R. Purshiana* DC. except for the narrower angles formed between the secondaries and midrib.

Rhamnus sp. Plate 11, fig. 3. The single leaf illustrated is the only one of the kind in the collection. No closely similar living equivalent has been found for it; but it is quite like some leaves of *R. cathartica* L. at the Michigan Botanical Gardens. Aberrant leaves of some species of *Prunus* are also somewhat similar. This would be a more logical living analogue than would be an European buckthorn. More material is necessary before anything other than conjecture is possible.

Ceanothus sp. Plate 10, fig. 5. The specimen illustrated, although broken, is quite suggestive of several species of *Ceanothus*. Because of its fragmentary condition no definite assignment to a living counterpart is attempted at this time.

Tiliaceae

Tilia parvulifolia n. sp. Plate 13, fig. 8. A single somewhat broken specimen and its counterpart appear to represent *Tilia*. It differs from LaMotte's specimens of *T. oregana* (24) in the fewer apparent secondaries which are also farther apart, in the lack of percurrent tertiaries, and in having coarser marginal teeth. The fragmentary nature of the material makes it impossible to be sure of the identification, but it is quite like several small-leaved species of *Tilia*. It is particularly like *T. floridans* of the southeastern United States.

Ericaceae

Arbutus idahoensis (Knowlt.) Brown. Plate 14, fig. 4. The Thorn Creek specimens, like those from Weiser, Idaho, are narrowly oblong, finely and regularly serrate, apparently quite thick with a stout midrib and numerous fairly conspicuous secondaries. In general aspect and venation this species is practically identical with *A. canariensis* L. It is more like this exotic species than any American type I have seen.

Arbutus opaca n. sp. Plate 14, fig. 1. Leaves coriaceous, narrowly obovate, narrowed gradually below to a long, slightly uneven base, the tissue of the blade decurrent on either side of the petiole for a distance of 1.8 cm. or more; blade rounded or acutish at the apex; margin entire; midrib stout, tapering, somewhat curved; secondary venation obscure, pinnate, secondaries very fine. 7 or more pairs arising at acute angles, somewhat sinuous, lost in the tissue of the blade before reaching the margin; finer venation an obscure irregular reticulum; length of largest specimen 6.8 cm. exclusive of the petiole; width 2.6 cm. Type 21519 U. M.

The more important characteristics of this species are the very obscure pinnate venation, lance-obovate shape and the extension of the blade along the petiole. These characters may all be duplicated in various species of *Arbutus*. but are not all evident in any one species so far studied. *A. Menziesii* Pursh often has the blade decurrent along the petiole, but its leaf is typically broadly oblong or ovate with a somewhat different type of venation. *A. arizonica* Sarg. and *A. texana* Buckl. conform somewhat better as to size and shape, but are usually widest below the middle. There is no indication of a wing on the petiole.

Two other species of *Arbutus*, *A. Matthesii* Chaney and *A. idahoensis* Brown, have been recognized in the western Miocene. Some authors do not differentiate between these two "species" but the specimens from Thorn Creek could scarcely be put in a single species. *A. idahoensis* appears to be a thicker leaf with quite prominent veins and a serrate margin. *A. Matthesii* is broader, may or may not be serrate and has its thin but distinct veins much farther apart than *A. opaca*.

Rhododendron idahoensis Smith. Leaves referred to this species are smaller than those of most living species of *Rhododendron*. The venation, however, appears to be similar and, until a more likely generic reference becomes evident, the best disposition to be made of the fossils seems to be to retain them in *Rhododendron*. This genus is a not unlikely constituent of a floral assemblage like that of Thorn Creek. Species of this genus are found in the northeastern United States and Appalachian region and in the humid Pacific flora.

Ebenaceae

Diospyros elliptica Knowlt. Plate 14, fig. 3. The small leaf illustrated appears to represent this species as figured by Knowlton (22) from Van Horn's Ranch in the John Day Basin of Oregon. Among living species, *D. texana* Scheele, the black persimmon of western and southern Texas and Mexico, is quite similar.

Oleaceae

Fraxinus leptocarya n. sp. Plate 12, fig. 2. Samara 1.6 to 1.9 cm. long, 3 to 4.5 mm. wide at widest point just above the middle; narrowed abruptly to point of attachment, round acute at other end; seed obscure, extending a little over one third the length of the samara; wing with very fine close-set parallel veins, often with a sharp ridge or line along the middle. Type no. 21523 U. M.

A number of living species of *Fraxinus* have a similar type of samara with a compressed obscure seed. Among these may be mentioned *F. Lowelli* Sarg., *F. anomala* Torr., *F. Bungeana* DC. and *F. quadrangulata Michx.* (Plate 12, fig. 3). This last species, which is found throughout the eastern United States, is probably closest to the fossil.

Caprifoliaceae

Symphoricarpos elegans (Lesq.) Smith. Plate 13, fig. 3. Although it has not been found abundantly in any fossil bed of the lower Snake River Valley, this species is now known from the Sucker Creek, Weiser and Thorn Creek beds. The wide-spread living species, *S. racemosus* Michx., from which the fossil leaves are indistinguishable, is common in the Thorn Creek Valley. It grows as a low spreading shrub so would not be expected to be abundant in fossil beds.

Fossils of Uncertain Taxonomic Position

Unidentified cone. Plate 3, fig. 16. This cone is quite suggestive of those of *Sequoia gigantea*, but the stem on which it is borne is remarkable. It is irregular and apparently bears numerous scars of leaves or branches.

Unidentified seed. Plate 2. fig. 10.

Unidentified catkin. Plate 9, fig. 4. Probably betulacous.

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A Consideration of the Structure of Lepidocarpon Scott Based on a New Strobilus from Iowa

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Introduction

Paleozoic lycopodiaceous strobili and their isolated parts have been the subject of intensive study by paleobotanists for over one hundred years. The criteria originally given as diagnostic for certain of these genera, and their modifications by later workers through the addition of new characteristics or the change in interpretation of established characteristics, present a confused picture of generic limitations. In this paper we will point out the intergradation and overlapping particularly of *Lepidocarpon* and *Lepidostrobus*, arising from modifications of original descriptions, both by direct statement and, indirectly, by assigning to one genus or the other, specimens which possess characteristics of both.

The main objective of this paper is to consider the diagnostic criteria of the genus *Lepidocarpon* as originally described by Scott (1900, 1901), and to illustrate the characteristics of the genus with new material. The contributions of more recent workers, Arnold, Bocheński, Darrah, Reed and Schopf will be considered insofar as their material concerns ours. It is not the purpose of this paper to approach a monographic study of the lycopodiaceous cone genera.

Material

The material on which this paper is based was collected by the authors as an isolated specimen in the Banner Coal Company's large strip mine about six miles north of Indianola, Warren County, Iowa, just east of U. S. Highway 65-69. Here the vein of coal is three to four feet thick and lies about fifty feet below the surface. It is in the Des Moines Series of the Pennsylvanian Period. The exact age has not been stated but Cline believes it is the same as the Lower Coal of Lugn's Lucas County report.[1] Coulter and Land (1911, 1921) and Matthews (1940) described some strobili of *Lepidostrobus Coulteri* Jongmans, from the same vicinity.

The specimen consists of a wedge-shaped fragment of a strobilus. From its external appearance we may be certain that we have the entire portion which was preserved. The specimen is carbonized over its entire surface. The preservation of the body of the specimen is excellent to within a few millimeters of the surface. It is calcified with a trace of pyritization. Distortion due to mineralization is negligible. A crystallization pattern occurs which may be sufficiently conspicuous to interfere with critical identification of structures when polished

[1] Cline, L. M., Iowa State College, Geol. Dept.—Personal Communication.

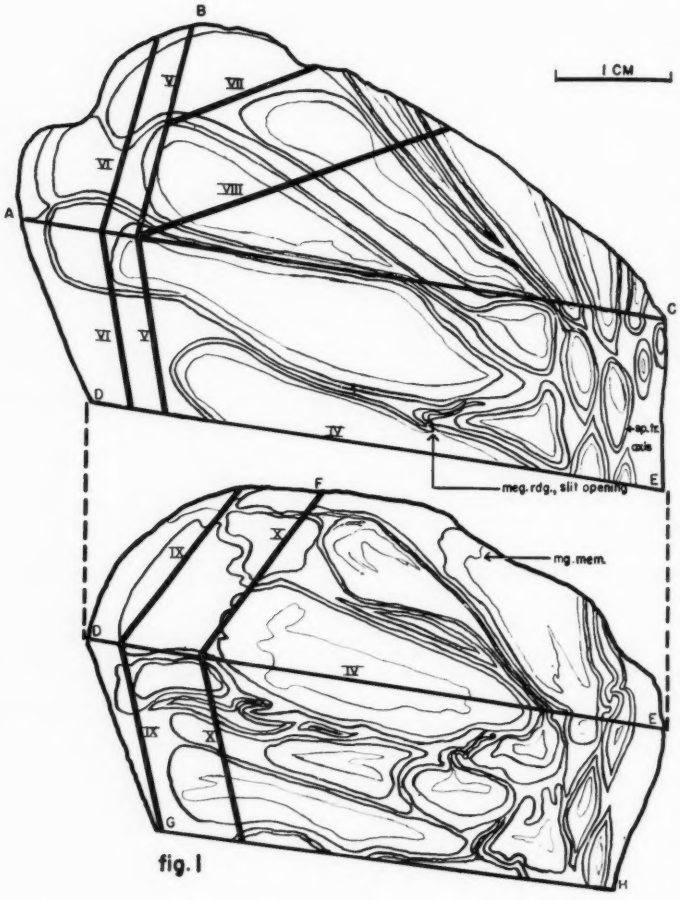


Fig. 1. Superimposed sketch of the upper and lower parts of the specimen of *Lepidocarpon ioense* after being separated by cut no. IV, showing surface features and position of cuts made in the study of the specimen. The axis of the strobilus is at the extreme right. Two transverse surfaces (to the strobilus) are lettered ABC and DFE. ABC was exposed by cut no. I and is near the top of the original specimen. The surface ACHG originally exposed by the obliquely radial cut no. II has been halved at DE by cut no. IV. The surface shown is in a plane intermediate between radial and tangential, and at the right passes through the outer cortex of the axis.

surfaces are studied by reflected light. The use of mounted peels in which all trace of rock matrix has been removed eliminates this problem.

The maximum dimensions of the specimen as found were about six and one-half centimeters high (parallel with the axis), five centimeters in radius (perpendicular to the axis), and three centimeters in width at the circumference (tangential to the strobilus as a whole). This latter dimension tapered evenly to the axis of the strobilus and the specimen thus presents a wedge-shaped surface when viewed from the top.

Significant measurements at the lower part of the specimen were distinctly less than at the upper; i.e., the strobilus tapered toward the base. Neither the apex nor the base of the original strobilus is present but the tapering of our specimen indicates that we have a portion of the lower half of the entire strobilus. According to our observations this fragment contained parts or all of at least twenty-four sporophylls and a portion of the axis. Probably this part was broken free from the rest of the cone before fossilization.

The measurements indicate that the strobilus was at least ten centimeters in maximum diameter and probably more than fourteen centimeters long. Even after a radial and two horizontal surfaces (top and bottom of the fragment) were exposed by cutting off irregularities and poorly preserved portions of the specimen the fragment measured over three centimeters high, with a radius of about five centimeters (Fig. 1). We know of no other specimen of *Lepidocarpon* as large. Even the large isolated "seeds" which have been abundantly collected, do not attain the over-all dimensions of thirty millimeters long by twelve millimeters high by fifteen millimeters wide as is found in many of our sporophyll invested sporangia.

In preparing the material for detailed study six cuts were made in addition to the original three which exposed one radial and two transverse surfaces. Each cut is numbered with a Roman numeral (Fig. 1), and the two faces which are exposed in each instance are designated as surface "a" or "b." A surface lettered "a" is either the surface nearer the axis in a tangential cut or a surface nearest the upper end of the strobilus in a transverse cut. A surface designated with the letter "b" indicates the most distal or lower surface exposed by the cut. Throughout this paper, unless specifically stated otherwise, sections, surfaces or cuts will be referred to in reference to their orientation to the strobilus as a whole rather than to the individual sporophyll or sporangium.

In making each cut an effort was made to expose certain structures with a minimum loss of material. This loss was made quite negligible by using No. 36 gauge steel or tinned wire, with No. 400 grade of Aloxite grinding powder suspended in water as the cutting agent. The specimen to be cut was first embedded in just enough sealing wax to hold it firmly. Sealing wax sets quickly, and is brittle when cool, so that it breaks away cleanly from the specimen without any damage, after the cut has been made. In this manner it is possible to hold the specimen absolutely rigid in a vise during cutting operations without danger of breakage. A further aid to cutting was devised in the form of roller guides through which the wire was drawn thus making the cut perfectly straight and smooth throughout. The width of the cut, i.e., the

section of material removed, was less than 160 microns. The exposed surfaces were then polished with the same abrasive as used for cutting. Nitrocellulose peels were taken from every surface. As many as twenty-eight peels per millimeter were taken in a series in order to trace the course of some of the more significant structures.

At first the peels were studied unmounted both under transmitted and reflected light. Later, however, the peels were washed for several minutes in five percent HCl to remove any inorganic material and then in water for a few minutes ot remove the acid. Each peel was then immersed in Eycleshymer's solution, which consists of equal parts of Bergamot and cedar oil in carbolic acid, for about two minutes prior to mounting in Canada balsam. There is no comparison in the amount of detail in the mounted and unmounted peels and also, in the mounted slides, the danger of misinterpreting mineralization pattern for cellular structure is obviated. Over two hundred slides were prepared during the study.

The eleven pieces of the specimen remaining after sectioning carry the University of Cincinnati Paleobotanical Museum serial numbers: 640 A-K. The slides are numbered according to section and surface numbers I-a, b—X-a, b and serial peels on each surface are numbered in order 1-28 or less. The sections are housed in the University of Cincinnati Paleobotanical Museum, Botany Department, where they are available for study. Several typical slides of the series are in the collections of the Illinois Geological Survey, the University of Notre Dame, and Dr. L. R. Wilson, Coe College, Cedar Rapids, Iowa.

Detailed Description of the Strobilus

Sporophyll

The strobilus is essentially of the *Lepidostrobus* type. A central axis bears numerous crowded sporophylls in a close spiral arrangement as indicated in tangential sections (Figs. 1, 7 and 8). The sporophylls are elongated perpendicularly to the axis and have a sharply up-turned distal extremity. The horizontal part of the sporophyll, the pedicel, bears upon its upper surface a single large, elongate, unilocular sporangium, which, in our specimen, is always enclosed by lateral extensions of the pedicel, the lateral laminae,[2] and by the up-turned distal extremity of the sporophyll, the distal lamina. This is a condition characteristic of *Lepidocarpon* and not known to occur in undoubted species of *Lepidostrobus*.

2 Scott (1900, 1901) and others have used the term "integument" for this investing structure on the basis that it is not a lateral extension of the pedicel but an additional, new structure arising from the superior face of the pedicel, enveloping the sporangium and forming an extended "micropylar slit" above the sporangium. Our material does not necessarily support this view. Tangential sections through the median portion of the sporophyll can scarcely be interpreted other than showing a lateral development of the pedicel, while sections taken distally and which show a somewhat different picture, can be readily interpreted in the same way. Furthermore, evidence at present does not show that archegonia occurred in the gametophyte located beneath the elongated "micropyle." We, therefore, minimize the use of the terms "integument" and "micropyle" in a sense other than descriptive. It is true that the lateral laminae are investing structures and form, therefore, an "integument."

The pedicel is strongly developed with a maximum width at the proximal end of six millimeters and at the distal end of from twelve to seventeen millimeters. In length it varies from two and one-half to three and one-half centimeters according to its position at the upper or lower part of our specimen. The distal region thickens considerably and together with the basal portion of the distal lamina is extended into a definite "heel." A conspicuous keel composed of rather thick-walled or sclerotic tissue extends from its decurrent attachment on the axis along the abaxial side of the pedicel throughout its entire length, rounds the "heel" and continues up the distal lamina for a short distance (Figs. 2, 4, 5, 8 and 12).

The main body of tissue of the pedicel is parenchymatous and relatively thin-walled. Scott (1901, p. 301) says that the tissue is more delicate toward the lower side which is scarcely the case in any of our sections, as there is a transitional area of strong tissue all along the lower side grading away from the sclerotic tissue which makes up the outer layer of the keel. This is indicated in Figs. 2, 8 and 12. A single, collateral vascular bundle traverses the entire length of the pedicel and at the distal end, gradually assumes a higher position, and passes into the erect distal lamina. In the median portion of the sporophyll, the vascular bundle is immediately beneath the attachment of the sporangium; at the proximal end, the bundle is slightly lower in the pedicel although well above the median line; distally, however, as the pedicel becomes more massive, the bundle is situated comparatively lower, at, or slightly below the central area (Figs. 7, 8, 12 and 16).

The vascular bundle is characteristic of the foliar organs of lycopods in general. The bundle area is conspicuous and essentially cylindrical, and while well defined from the adjacent mesophyll in general, exact delimitations are difficult to determine. The xylem is linear or ovoid in outline as seen in tangential section and is made up of tracheids with either spiral or scalariform markings. Protoxylem cannot be identified with any degree of accuracy, but in some instances at least, the smallest tracheids occur near the lateral extremities of the trace, but apparently with at least one larger cell intervening between them and the surrounding parenchyma. The trace is probably mesarch as Scott indicated.

The phloem area is often preserved but more frequently its position is indicated only by a lacunar area. Between the xylem and the phloem is a thin parenchymatous layer. Surrounding both xylem and phloem is a zone of thin-walled parenchyma which seems to grade into an indefinite sheath of thicker-walled tissue. No transfusion tissue was observed in this region.

There is no indication of any direct vascular supply to the base of the elongated sporangium.

In nearly all tangential sections two areas of large, thin-walled parenchyma, which is often badly broken down or represented only by lacunar openings, are found parallel to the vascular bundle (Figs. 2 and 12). These have been observed by Scott (1901) and Reed (1936), and are no doubt of parichnos nature. These areas are distinct in the terminal lamina, at least in the basal part. There the thin-walled parenchyma is not so badly broken down, however.

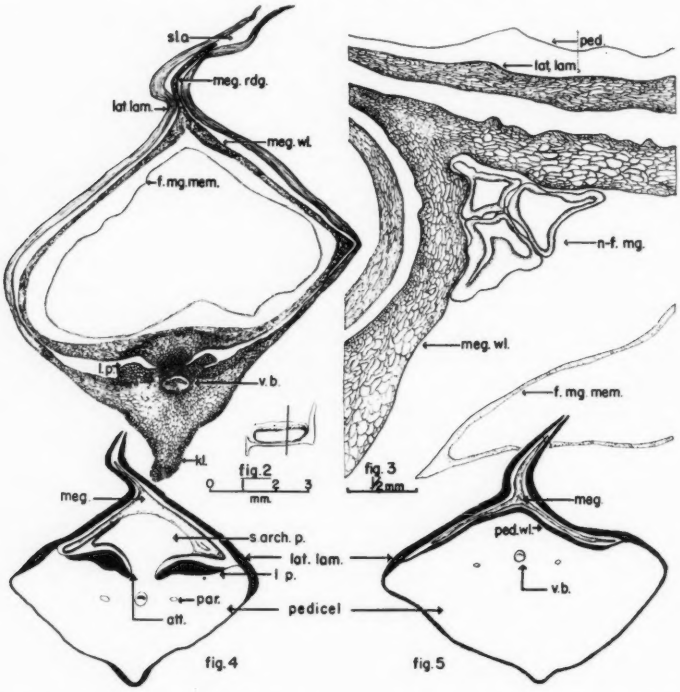


Fig. 2. Sketch showing typical tissue arrangements, parts and structures of a single megasporophyll and sporangium as seen in a section tangential to the strobilus. Position and plane of cut are indicated by inset. sl.o., slit-like opening; meg. rdg., megasporangial ridge; lat. lam., lateral lamina; meg. wl., megasporangium wall; f. mg. mem., functional megaspore membrane; s. arch. pad, sub-archesporial pad; l.p., lateral pad; v.b., vascular bundle; par., parichnos area; ped., pedicel; kl., keel.

Fig. 3. Camera lucida drawing of a tangential section through distal end of megasporangium. The characteristic appearance and position of the three non-functional megaspores (n-f. mg.) of the tetrad are indicated in relation to the functional megaspore wall (f-meg. mem.). Slide no. 640-Vb-2.

Fig. 4. Diagram of transverse section of sporophyll near distal end of sporangium. Basal tissue of sporangium fills much of cavity (meg.) which here is reduced to a narrow three-lobed structure. The origin of the lateral laminae (lat. lam.) is clearly at the lateral margins of the pedicel.

Fig. 5. Diagram of a section of sporophyll beyond that shown in Fig. 4 and distal to the sporangial attachment to pedicel. The free tip of the sporangium (meg.) extends for a short distance in an extremely trilobed form, the inner sporangial wall apparently closing the sporangium cavity. All traces of the basal tissues of the sporangium are lost. The superior face of the pedicel (ped. wl.) extends upward into the space between two of the sporangium lobes. The lateral laminae become free high on the superior face of the pedicel, but their origin from the lateral edges of the pedicel is apparent.

A tissue of the pedicel prominent throughout its entire length is the sclerotic tissue situated on either side of the sporangial attachment. These areas have been variously designated, but Scott's (1901) original terminology "lateral pads," is the most effective and least committal of any. Their occurrence may be correlated, most probably, with the function of supporting the large sporangium immediately above (Figs. 2, 12 and 16). These lateral pads are not equally conspicuous nor is their arrangement identical throughout the length of the pedicel. In general, they are least conspicuous at the extreme proximal end. Elsewhere they may appear as definite lobes of tissue distinctly raised above the superior face of the pedicel, or they may be as strongly developed, but contained within shallow depressions or horizontal grooves on the upper surface of the pedicel and scarcely or not at all extending above its surface. In one instance the sporangial stalk arises from a shallow pocket or groove, the sides of which are formed by these lateral pads; in the other the sporangium is essentially sessile and no such pocket occurs.

A ligule is borne on the upper surface of the pedicel just beyond the most distal point of attachment of the sporangium. This position is shown in radial section in Fig. 6 and in tangential section in Fig. 16. The widest dimension in

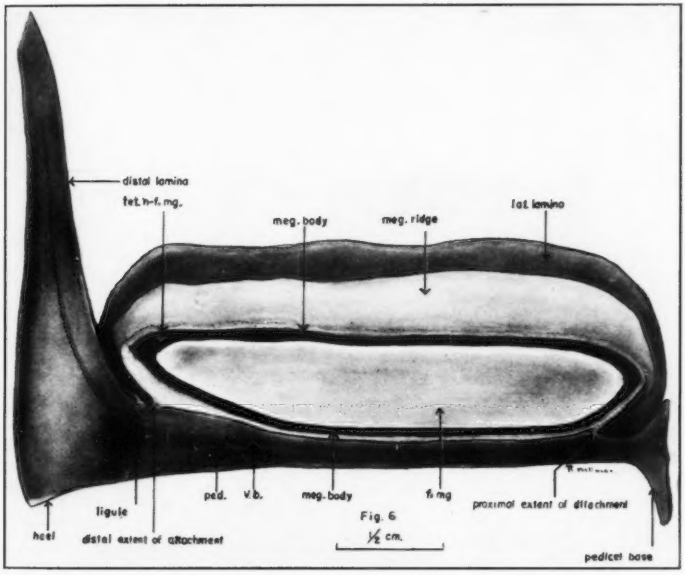


Fig. 6. Reconstruction of a radial section through the sporophyll and sporangium of *Lepidocarpon ioense*. The lateral lamina is shown overlapping the sporangial ridge. The large functional megaspore (f. mg.) in the slightly larger megasporangium (meg. body) and the three non-functional members of the tetrad (n-f. mg) appear in their correct position at the upper distal end of the megasporangium cavity. The ligule is distal to sporangial attachment.

Fig. 7. Section through strobilus intermediate between tangential and radial. At the left are the ovoid sporophyll traces in outer cortex of axis with vascular bundle (v.b.) and indications of the sporophyll base (sp. tr.); at the extreme right are sporangia in characteristic outline; intermediate are sporophyll bases with some indication of sporophyll tissue. The traces at the extreme left are almost tangential to axis; the sporophylls at right are intermediate between tangential and radial. Spiral arrangement of sporophylls is indicated. Slide 640-II b 3.

transverse section of the ligule is about 450 microns. An interesting problem was involved in finding and properly identifying the ligule in this specimen. Several structures were found approximately in the correct position which simulated the true ligule. Had our sections been limited in number in place of a complete series the correction of these potential errors would have been extremely difficult or impossible. This was not the only instance in which the advantage of long series of peels was demonstrated. Interpretations based on a minimum number of sections must be most carefully drawn.

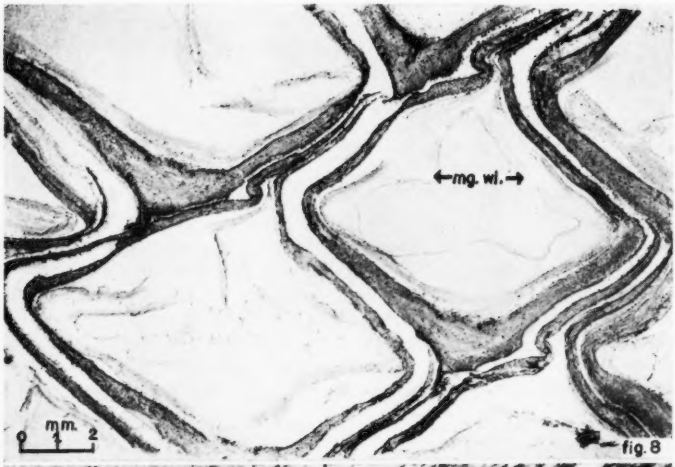
The lateral laminae arise directly from the lateral margins of the pedicel where they are, naturally, the thickest, and thin out gradually to their edges (Figs. 2, 8, 9, 10, and 11). They follow closely the contour of the invested sporangium, their edges extending well above the sporangium in essentially parallel planes forming a narrow slit or elongated opening (Scott's micropyle). In tangential sections the laminae may be seen to have a remarkably constant, peculiarly curved arrangement. The diagrammatic sketch in Fig. 6 illustrates the relationship of the lateral laminae to the pedicel and sporangium.

The structure of the lamina is not complex. A small-celled epidermis covers both surfaces. These cells are rather heavy-walled. Toward the center of the lamina the cells are larger and the walls are thinner. They are essentially isodiametric, but frequently show some elongation vertical to the pedicel (Figs. 9, 10 and 11). Fig. 12 shows a situation in which, during the development of the lateral laminae, the edge of one lamina went to one side of the keel of the next sporophyll above, while the edge of the second lamina became entangled with the base of the keel, the tip bending into a shepherd's crook when viewed in tangential section (cross section of sporophyll).

Tangential sections taken at the extreme proximal end of the sporophyll fail to demonstrate a complete and unbroken enclosure by the laminae as has been suggested for other species by Scott (1901). The evidence from this specimen is that the top edges of the lateral laminae are distinct throughout from their proximal extremities. Under any circumstances the distance from the periphery of the cone axis radially until the structure of the sporophyll is typical of the more familiar medial region cannot be more than two millimeters and may be less. It would rather appear that the lateral laminae at their proximal extremities are closely appressed to the sporophyll base, perhaps even continuous with it, and together form the proximal covering of the sporangium.

The organization of the sporophyll at its distal end presents quite a different picture from that already described (Figs. 4 and 5). The pedicel becomes greatly thickened, the lateral pads extending almost to the base of the lateral laminae. The laminae themselves are not as strongly developed as in more medial sections, and, in place of departing from the pedicel at a wide angle (Fig. 5), as is characteristic elsewhere on the pedicel, they bend in sharply, lying closely appressed to the reduced sporangium. This gives the appearance described by Scott (1901) and others of the investing structures arising not from the lateral edges of the pedicel, but from its superior face.

In our specimen a consideration of the histology of the laminal tissue



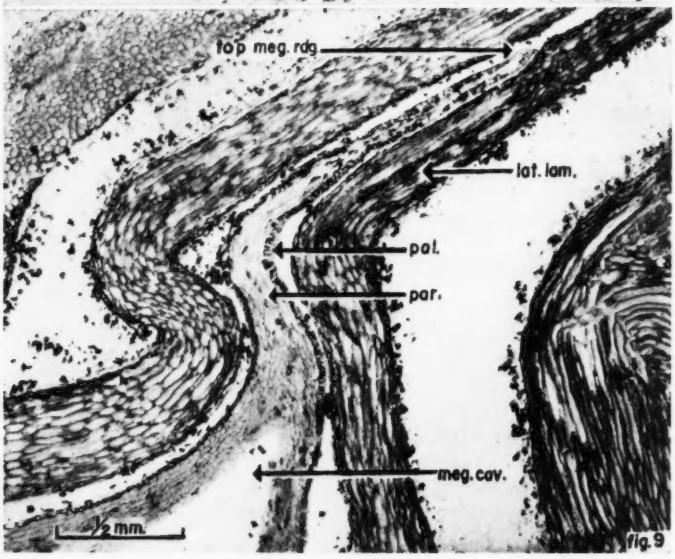


Fig. 8. Section tangential to strobilus showing essentially transverse sections of several megasporophylls and megasporangia about midway between distal and proximal ends. Slide 640-VIII A 3.

Fig. 9. An enlarged detail from Fig. 8; lat. lam., lateral lamina; pal., the palisade-like outer layer of the megasporangium wall; par., the inner parenchymatous wall layer; meg. cav., megasporangial cavity; the unbroken character of the sporangial wall throughout the megasporangial ridge is evident (top meg. rdg.)

clearly indicates that distally, just as in more median portions, the lateral laminae are extensions of the lateral parts of the pedicel, are reduced in size and changed in orientation, and follow as usual the contour of the sporangium until they finally disappear as they merge with the fleshy base of the up-turned distal lamina.

There is no evidence to indicate the occurrence of other lobes or tangential extensions of the pedicel that could be considered as lateral extensions of the pedicel other than these investing structures. Their appearance on the superior face of the pedicel in distal sections clearly represents a growth habit. There is no reason to assume, from a study of this specimen, that Scott's integument is other than a normal laminal lateral outgrowth of the pedicel.

An extreme example of the reduction of the laminae distally and their apparent origin from the superior face of the pedicel is represented in Fig. 5. This is a diagrammatic sketch of a tangential section through the distal end of the sporangium near the distal lamina. The sporangium is free from its attachment. The upper surface of the pedicel, rising sharply to join the distal lamina, completely fills the area beneath the trilobed sporangium.

The up-turned distal laminae of the sporophylls are not completely known in our specimen as none of them extend more than two centimeters vertically. The tips have all broken away. This lack of preservation might indicate that the upper parts of the distal laminae were poorly developed structurally and thus readily lost, or that there was a zone of weakness, or might indicate that the upper parts were less imbricate than the lower two centimeters which are preserved. The basal portion is closely appressed and overlaps in part the bases of the sporophylls immediately above.

The angle formed by the distal lamina to the sporophyll pedicel has often been used as one of the criteria in designating species. If we can assume the angle formed by the basal remnant of the lamina is correct for the entire distal portion we can say that it forms an angle of about seventy-five degrees with the plane of the pedicel.

Sporangium

The sporangium is a radially elongated structure seated upon the upper surface of the sporophyll pedicel. A conspicuous ridge, which is a narrow vertical extension of the sporangial chamber, extends along the entire top of the sporangium. The sporangium, including this sporangial ridge, is enclosed by the lateral laminae except for a narrow slit at the top.

The radial dimension of the sporangium varies from two and one-fourth to three centimeters. It is narrow near the axis of the strobilus and broadens out distally. The form and outline of the sporangium was determined by means of sections tangential to the axis (Figs. 2, 4, 5, 7, 8 and 10); radial sections (Figs. 1 and 6); and transverse sections (Figs. 1 and 14). The proximal sections tangential to the axis and sections of the same sporangium taken somewhat further from the axis, show the sporangium to be rhomboidal in outline with the dorsal ridge (megasporangium ridge) extending for several

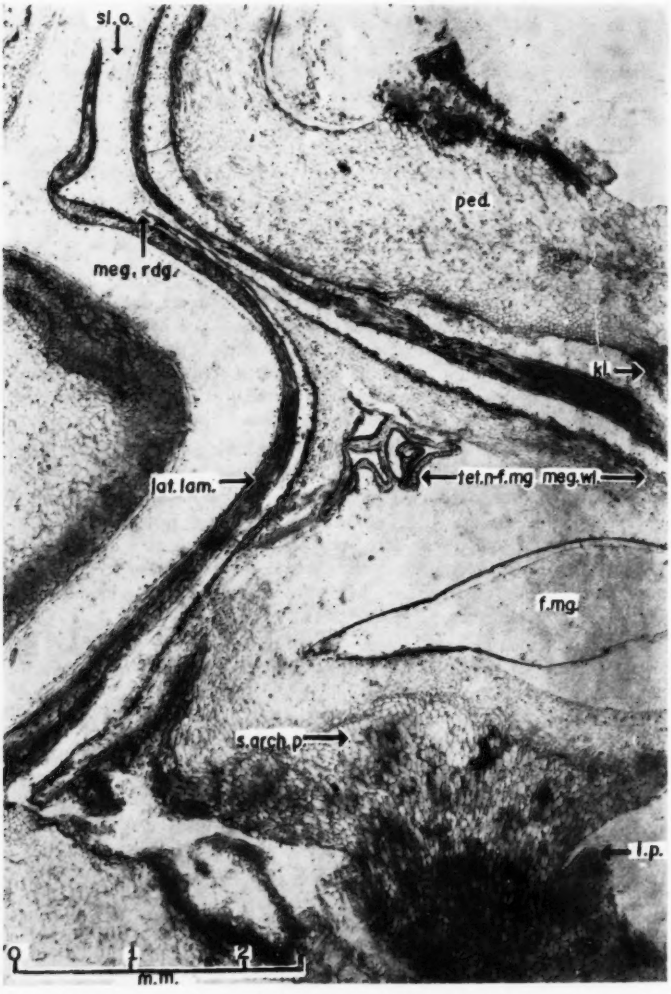


Fig. 10. Section nearly tangential to axis near the distal end of the sporangium. The "saddle-bags" or trilobed appearance of the distal end of the sporangium is just beginning to appear. l.p., lateral pads; s. arch. p., sub-archesporial pad; lat. lam., lateral lamina; f. mg., functional megaspore; tet. nf. mg., non-functional megaspores in tetrad formation; meg. rdg., megasporangial ridge; sl.o., slit-like opening between lateral laminae; kl., and ped., keel and pedicel of adjacent sporophyll. Slide no. 640-Vb 3.

millimeters above the main sporangial cavity. More distally both the upper surface of the pedicel and the base of the sporangium gradually become flattened, the sporangium being triangular in section.

From approximately the position of the ligule to near the distal extremity, the upper surface of the pedicel is strongly convex, conforming to the "saddle-bags" appearance of the sporangium. The relative position of tissues is shown in the diagrammatic reconstruction (Fig. 6). At the extreme distal end the sporangium assumes an interesting triradiate shape (Fig. 5) which we will discuss later.

The sporangium is attached to the sporophyll by a narrow basal tissue nearly throughout its length. It is unattached distally beyond the position of the ligule, i.e., about three to five millimeters of its distal end (Figs. 6 and 16). There is some variation in the width of the attachment. Near the axis it is approximately one millimeter wide. This gradually increases to about two millimeters midway between the proximal and distal ends and remains fairly constant until within one or two millimeters of the distal end where it tapers abruptly. Fig. 13 shows the relative position of the tissues at the most distal point of attachment. In the next peel of the series the sporangium is no longer attached to the pedicel. In transverse sections of the individual sporangium the attachment appears either as a short stalk or the sporangium is essentially sessile on the pedicel (Figs. 2, 10, 13, 12, and 8 respectively).

The wall of the sporangium is composed of an outer layer of narrow, columnar, prismatic cells elongated vertically to the surface of the sporangium, and an inner layer, ten to fifteen cells in thickness, composed of larger, thin-walled cells not as strongly developed as the mesophyll of the lamina which encloses it. (Compare the two tissues in Figs. 8, 9 and 11). This thin-walled parenchymatous inner wall tissue apparently is a permanent part of the sporangium wall and not a temporary or tapetal tissue. It extends completely across the basal portion of the sporangium, and, unchanged, although in lesser amount, to the very tip of the megasporangial ridge contrary to the evidence presented by Scott (1901, p. 298) (See Fig. 9). A hand lens may be used profitably in studying the photograph. It is to be noted that the tissues of the megasporangial ridge are intact throughout, except where they have been obviously broken by mineralization. There is no indication in our material that an opening to the sporangium was ever normally effected through the megasporangial ridge.

The basal region of the sporangium is divided sharply into an upper (inner) parenchymatous layer continuous with the inner wall layer of the lateral walls and ridge, and a lower tissue, cone-shaped in section, which extends downward to the sporangial attachment, the sub-archesporial pad. The cells of this tissue are large and firm and excellently preserved, and are so arranged that when seen in transverse section of the sporangium they appear to radiate from the pedicel toward the sporangial cavity (Figs. 2, 10, 12 and 13).

The degree of development of this basal tissue between the sporangial

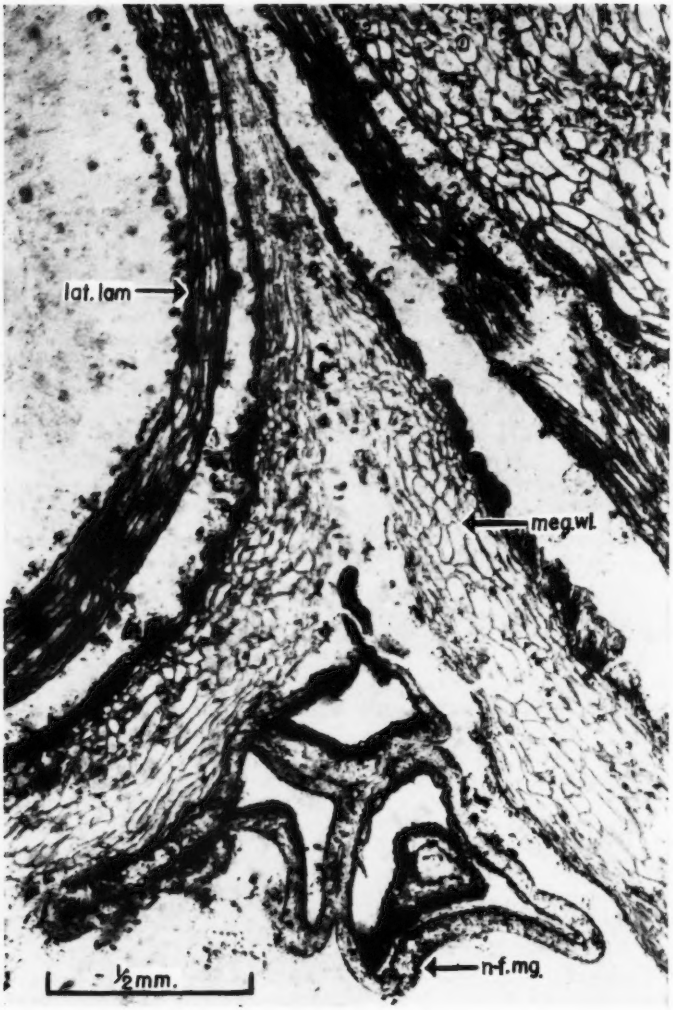


Fig. 11. Enlarged detail of part of Fig. 10. The three non-functional megaspores are shown in contact in the tetrad position (n-f. mg.); the megasporangium wall (mg. wl.), the megasporangial ridge and lateral laminae, (lat. lam.) are shown in characteristic position.

attachment and sporangial cavity varies with the distance from the sporophyll attachment on the axis. Proximally the development is slight, almost insignificant; through the medial regions, a definite hump extends into the basal part of the sporangial cavity; distally, however, this tissue gradually fills the sporangial cavity resulting in a striking inverted Y appearance, the sporangial ridge forming one arm of the Y. Fig. 4, a diagram taken from one of a long series of sections shows the partial filling of the sporangial cavity by the encroachment of this basal tissue. Distally to the sporangial attachment the three-lobed form of the sporangial tip persists for a short distance.

It is possible that entrance into the sporangium was accomplished through this triradiate distal extension of the sporangium, which terminates very close to the adaxial surface of the distal lamina. It may be significant that spores of undetermined identity were found only in the most distal portion of the sporangium.

Sections transverse to the strobilus present some interesting problems of interpretation. A normal situation is illustrated in Fig. 14. Because of the crowded position of the sporophylls on the axis a single section may pass through the sporangial ridge of some, through the middle or lower parts of others, while some sporangia have only a trace showing. This situation may occur when the section has not been actually transverse to the strobilus, or when the sporangia themselves are not borne exactly at right angles to the cone axis, or when there are inequalities of growth of the sporangia themselves. In any event, a section through the sporangium such as the one parallel to and adjoining the bottom of Fig. 14 must be correctly interpreted. The apparent distal attachment of the sporangium is produced by the plane of the section passing through the distal portion of the pedicel. The vascular bundle is the bundle of the pedicel and not that of the distal lamina. Thus the section, which was cut as nearly transverse to the cone axis as possible, shows an oblique section through that particular sporophyll and sporangium. This situation may be duplicated in our sections as many as twenty times. In some of them it is most difficult to identify such a section which is intermediate between transverse and tangential from a true tangential section. We can identify such oblique sections by their vertical elongation of the sporangia in which they appear to be distinctly higher than wide, a condition which does not actually exist in our material. In such oblique sections the vascular bundle often appears to have been sectioned nearly transverse. Surely the possibility is very great that sections of a single sporangium and sporophyll figured by Scott and others as transverse to the sporangium itself (tangential to the cone axis), and which indicate that the sporangium is much higher than wide, are in reality oblique sections, intermediate between transverse and tangential to the cone axis.

We have found no instance in any of our many sections which are truly tangential to the cone axis where a vertical elongation of the sporangium occurs, except sections at the extreme proximal end of the sporangium which do not show a typical organization. Size and organization readily identify these. One common explanation suggested for such apparent vertical elonga-

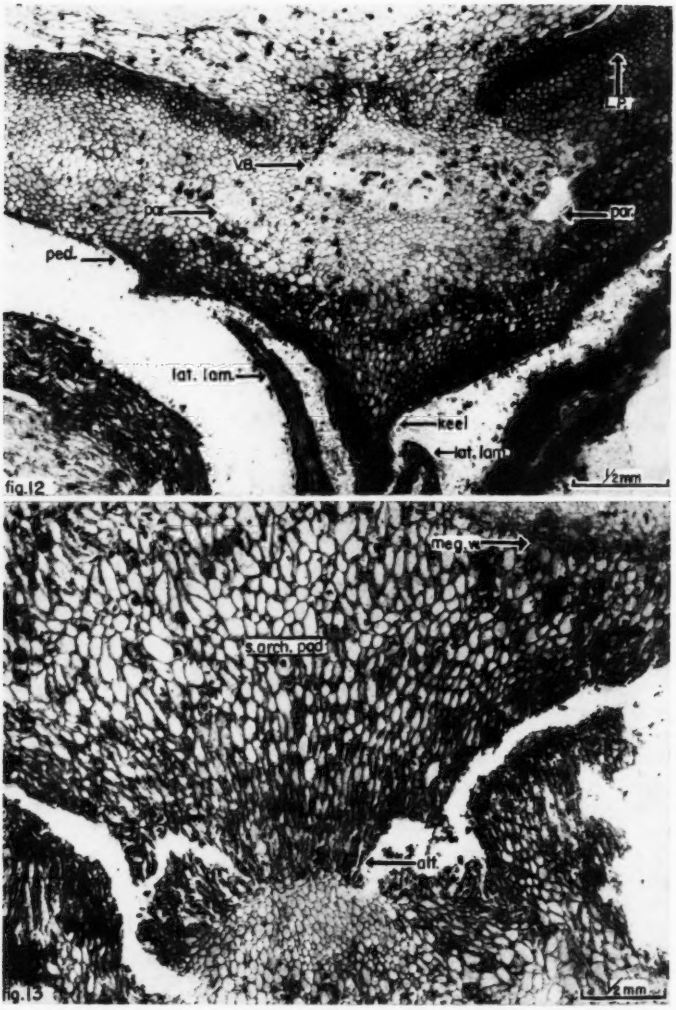


Fig. 12. Transverse section of pedicel and base of sporophyll near the proximal end of the sporangium. Slide no. 640. VIIIa 3.

Fig. 13. Detail of sporangium attachment more distally than in Fig. 12. Inner parenchymatous wall layer of sporangium, continuous over base of sporangial cavity, indicated at meg. w. Slide no. 640 Vb 16.

tion has been the popular idea that only certain of the sporangia produced functional spores resulting in a distortion due to unequal pressure on the sides and top. Our material cannot support this idea. Every visible sporangium has developed normally. Further confusion as to the normal outline of the sporangium in sections truly transverse to the sporangium itself (tangential to axis) has arisen following the reproduction by some authors of illustrations as "transverse," originally figured by Scott, which he himself stated were only *approximately* in that plane (Scott 1901, Fig. 10).

Spores

It seems clear that in *Lepidocarpon* but one functional megaspore mother-cell developed. In this study we have been able to show the occurrence of four megaspores in each of four sporangia. In each instance one spore of the four may properly be considered a functional megaspore. In two of the sporangia the three non-functional spores are still in contact in typical tetrad formation but are free of the functional spore (Figs. 3 and 11). In the other two sporangia the non-functional spores are quite distinct but are slightly scattered in the upper part of the distal end of the sporangium (Figs. 14, inset, and 15). The position of the non-functional spores in the sporangium is apparently quite constant, whether in the tetrad formation or scattered, and are always to be looked for at the distal end of the sporangium near the upper wall. Their position in relation to the position of the ligule is indicated in Fig. 6.

While the complete tetrad of spores was found in but four sporangia (no doubt further sectioning would expose others), the functional spore is present in each sporangium sectioned, essentially similar in size and position.

There is some evidence that the three non-functional spores of the tetrad continue enlargement for at least some time after tetrad formation. Those that are yet in contact with each other measure approximately 750 microns in diameter (Figs. 3, 11 and 10). Those which are no longer in contact with the others, but are dispersed, may have a diameter as great as 900-1000 microns. All the non-functional spores have walls quite thick (Figs. 3 and 11). However, those yet in tetrad formation are slightly thicker than those which have separated (Fig. 15). All the non-functional spores have walls thicker than that of the large functional spore. The increase in size and the slightly thinner spore wall of the dispersed spores would seem to indicate some tendency on the part of all four spores to continue development. One can suppose, possibly, that for either the lower or the proximal member of the tetrad, if such a designation is either possible or necessary, conditions within the individual sporangium were such as to favor continued development of that single spore, but not of the remaining three, although obviously, the habit of a single functional megaspore was firmly established in this genus.

The functional megaspore nearly fills the sporangial cavity in all observed instances. The wall is rather thin and uniform except possibly at the distal end where sometimes it appears to be thicker. This appearance may be due to the section passing obliquely through the curving terminal wall. The suggestion

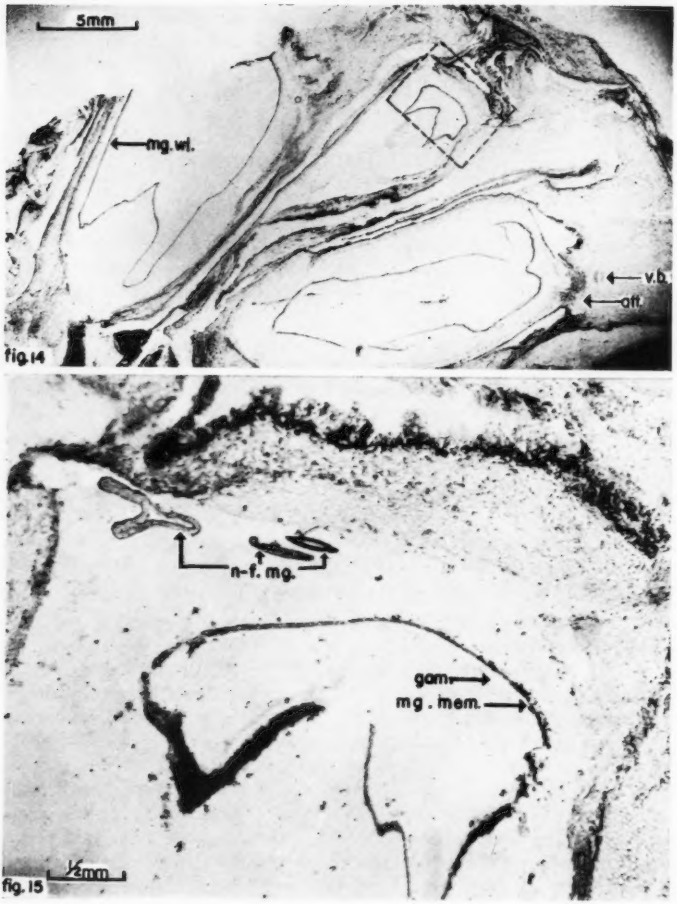


Fig. 14. Section cut intermediate between transverse and tangential. The sporangial attachment (att.) is apparently distal, but indicates merely the oblique nature of the section. The vascular bundle (v.b.) is the bundle of the pedicel near the distal lamina, but not the bundle of the lamina. The megaspore wall is shown in three megasporangia (mg. wl.). Slide no. 640-IVb 2.

Fig. 15. An enlargement of inset shown in Fig. 14; n-f. mg., the three non functional megaspores not in contact; gam., evidences of female gametophyte tissue within the large megaspore (mg. mem.).

that the wall has merely stretched to accommodate the growth of the gametophyte within has fair substantiation. Scott's characterization of the functional megaspore wall as being a brown structureless (non-cellular) membrane is adequate.

Although the wall is thin it is generally preserved essentially intact. The normal shape and position of the functional spore are indicated in the reconstruction (Fig. 6) and its position in transverse section of the sporangium at various distances from the axis may be observed in Figs. 1, 2, 7, 8 and 10. In a few sections the spore wall was wrinkled or collapsed before or during petrifaction and may be so lobed at the distal end that sections through one of these lobes give an excellent appearance of a dispersed non-functional spore and can readily be mistaken for one.

The structure of the spore wall is essentially the same in the functional and non-functional spores, but vary sufficiently in the form of the minute units making up the wall to make recognition usually reliable. In the spores yet in the tetrad position, these units are granular, irregular globose or ovoid in appearance. In the dispersed spore wall these particles are less smooth, more elongate; the thin wall of the large functional spore is composed of definitely elongated branching and interlocking fibrils. There are, of course, all intergradations and probably the distinctions suggested do not always hold.

Careful observations revealed no indication of a triradiate structure on the wall of the functional megaspore. Similar observations of the non-functional spores in tetrad position gave merely a suggestion of such a structure. If this suggestion is correct, triradiate markings occur on the inner or adjacent walls of the spores. If this is true we might expect to find some evidence of a triradiate opening at the distal end of the functional spore, adjacent to the peculiar three-lobed distal extension of the sporangium.

Evidences of gametophytic tissue occur in nearly every megaspore. In no instance, however, is it well preserved. Usually it is found as a thin layer roughly paralleling the megaspore wall. The best development of the tissue observed is in sections through the distal end of the spore. It is probable that gametophytic tissue was extensive in these spores and has been lost in preservation.

Axis

The axis is represented by a part of the peripheral tissues only, no part of the central vascular cylinder being present. Peels do, however, give an interesting series of views of the sporophyll base and trace as seen in sections cut intermediate between tangential and radial (Fig. 7). At the right in this illustration may be seen a part of a nearly vertical row of sporophylls (the sporophylls are obviously spirally arranged) with lateral laminae and bearing sporangia. This row is definitely cut in a plane intermediate between tangential and radial (to the axis). To their left is a part of a second row of sporophylls cut through the pedicel base and showing parts of the lateral laminae and occasionally fragments of the proximal ends of the sporangia. At the left of

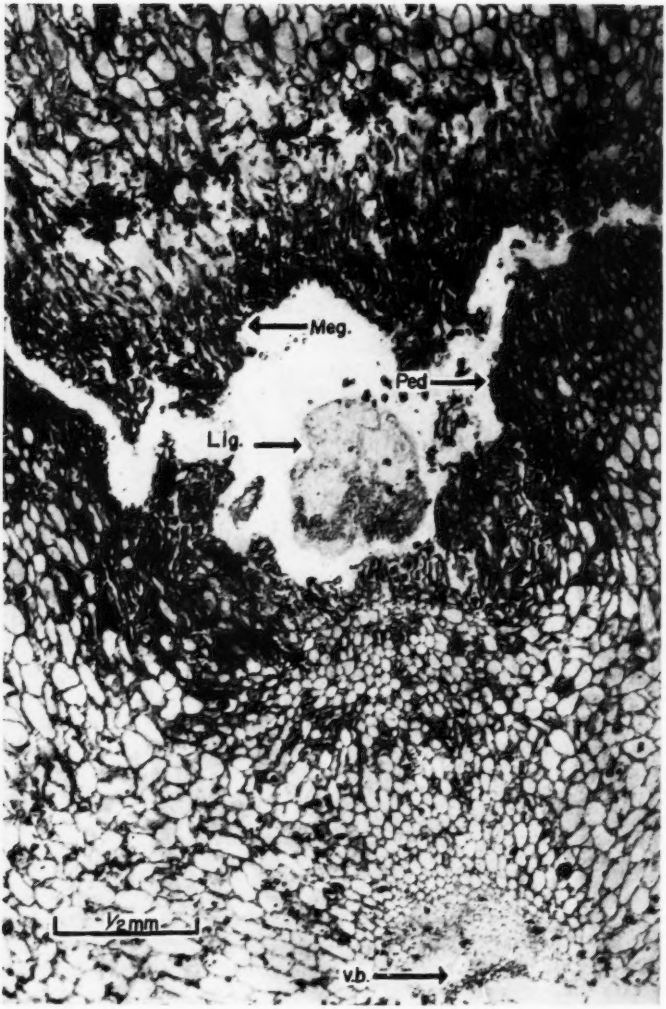


Fig. 16. Transverse section of sporophyll at position of ligule (lig.); v.b., vascular bundle; ped., superior face of pedicel; meg., basal portion of unattached sporangium. Slide no. 640 Vb 26.

the illustration are parts of two rows of sporophyll traces which appear as vertically elongated ovals, with the vascular bundle centrally placed. Those at the extreme left are cut deeper in the cortex of the axis than are the second row, and consequently smaller. These represent the innermost part of the strobilus represented in this specimen.

The vascular bundle is similar to that seen in the pedicel. The xylem elements are small, with spiral and possibly scalariform markings. The phloem cannot be distinguished, its position usually represented by a lacunar opening. Surrounding the vascular strand is a relatively large area of thin-walled cells, larger than the xylem elements, uniform in size and character. Some of these cells, especially above the sporophyll trace, have characteristic xylem markings. They are suggestive of transfusion tissue.

Lepidocarpon ioense sp. nov.

Strobilus: Large, more than ten centimeters in diameter, at least fourteen centimeters long and probably much longer, tapering toward the base.

Axis: Outer cortex, showing spiral arrangement of sporophylls, only part of axis preserved. Sporophyll trace typical, vascular bundle collateral, surrounded by zone of parenchyma and sheath.

Sporophyll: Megasporophylls crowded, arranged in a close spiral, attached nearly at right angles and elongated vertically to the axis for two and one-half to three and one-half centimeters to the up-turned distal lamina. Tips of distal laminae regularly lacking after approximately two and one-half centimeters. Pedicel extended abaxially to form a conspicuous keel throughout, merging with the heel of the distal lamina. An unbranched collateral vascular bundle, traversing the outer cortex, enters the base of the sporophyll and continues throughout its known length. Lateral laminae extend around and above the sporangium, and together with the distal lamina, form an investing structure. Lateral laminae, in tangential section, extend about twelve millimeters from their attachment on the pedicel, approximately five of which extend above the sporangial cavity, exceeding the sporangial ridge in height by some two millimeters. Lateral laminae, proximally, in close contact with sporophyll base; distally they merge with distal lamina.

Ligule: Ligule present on adaxial surface of sporophyll immediately distal to sporangium; about 450 microns in greatest width and over one millimeter in length.

Sporangium: Megasporangium large, two and one-fourth to three centimeters long, sporangial cavity approximately seven millimeters high, the sporangial wall extending vertically for about two and one-half millimeters forming the megasporangial ridge; sporangium attached for approximately its entire length along the adaxial surface of the sporophyll pedicel, either stalked or essentially sessile, resting on "lateral pads"; sub-archesporial pad increasingly conspicuous distally; distal end of sporangium extends beyond attachment in a characteristic three-lobed extremity, the megasporangial ridge forming one lobe, the other two initiated by extensive development of sub-archesporial pad.

Spores: Four megaspores are present in each megasporium resulting from the divisions of a single functional megaspore mother-cell. Three of these are non-functional, 750-1000 microns in diameter, regularly occurring in the upper part of the sporangial cavity at its distal end; at first remaining in contact in typical tetrad formation, later becoming dispersed. One functional megaspore, very large, nearly filling the sporangial cavity; wall thin and uniform.

Gametophyte tissue: Evidences of gametophyte tissue present in most megaspores, apparently more strongly developed toward distal extremity.

Location and horizon: From coal of Des Moines Series, Pennsylvanian Period, six miles north of Indianola, Warren County, Iowa; Banner Coal Company strip mine.

Material: One calcified specimen, a wedge-shaped section of the lower part of a strobilus, cut into eleven parts from which about 200 peels were taken; housed in Paleobotanical Collection, Botany Department, University of Cincinnati.

Name of Type: Lepidocarpon ioense, indicating the geographical source of the material.

Discussion

Lepidocarpon was established as a genus (Scott 1900) to include some previously misinterpreted cone material. (Williamson 1877). Scott's generic diagnosis was revised (Scott 1901) to read as follows:

Lepidocarpon, gen. nov. (Scott)

Strobili, with the characters of *Lepidostrobus*, but each megasporangium inclosed, when mature, in an integument, growing up from the superior face of the sporophyll pedicel.

Integument, together with the lamina of the sporophyll, completely enveloping the megasporangium, or nucellus, leaving only an elongated, slit-like micropyle above. A single functional megaspore or embryo-sac developed in each megasporangium and occupying almost the whole of its cavity.

Megaspore ultimately filled by the prothallus or endosperm.

Sporophyll, together with integumented megasporangium and its contents detached entire from the axis of the strobilus, the whole forming a closed, seed-like, reproductive body.

Seed-like organ horizontally elongated, in the direction of the sporophyll pedicel, to which the micropylar crevice is parallel.

Scott, in the same work, also says:

"The comparison of specimens in the two conditions"—(immature, lacking the enclosing lateral laminae, and mature with the laminae) "has shown the relation of the seed-like organ of *Lepidocarpon* to the ordinary megasporangium of a *Lepidostrobus*. The former differs from the latter in two principal respects: —

(1). It contains only one functional megaspore, which like the embryo-sac of an ovule or seed, occupies almost the whole interior of the megasporangium, but is accompanied by the three other spores of the tetrad in an abortive condition.

(2). When mature, the megasporangium of *Lepidocarpon* is enclosed by an integument, which is a new formation, growing up from the tissue of the sporophyll, and forming, together with the latter, a complete envelope to the sporangium, only open by a narrow micropylar crevice along the top.

The essential features upon which this generic diagnosis was based have been largely substantiated by our observations. It may be expected that the designation of any form genus will be elastic enough to receive a few irregular species. In recent works, however, first one and then another exception has been taken until, in culmination, if these exceptions are to be followed, significant diagnostic characters of this genus scarcely exist.

Darrah (1941B), in his new species, *Lepidocarpon glabrum*, which occurs abundantly as isolated seed-like bodies in the coal ball flora of Iowa and Kansas (Darrah 1941A), has cited an instance in which a mature sporangium is shed free of its sporophyll. In general external appearance he describes these bodies as being "smooth and lustrous" and without any prominent scars or markings. He has shown that, structurally, this type is essentially a sporangium with a wall of thickened cells, with no apparent mechanism for dehiscence. He has also shown that these sporangial bodies conform in general character to the portion of Lesquereux's genus *Lepidocystis* (Lesquereux 1880) represented by *L. vesicularis* Lesquereux. This type has a bladder-like, oval or squarish, sporangium containing a large spore as contrasted to the type of *L. fraxiniformis* Lesquereux which has a sporangium containing many spores.

It is Darrah's contention that this species, *Lepidocarpon glabrum* Darrah, represents a "more mature condition of the seed body than is usually observed in the familiar *Lepidocarpon*" (Darrah 1941B). In discussing these sporangial bodies from the Iowa coal balls he states that only the smaller and more immature forms are recognized as typical and that "all of the seeds attaining a maximal or near maximal size are found isolated." He substantiates this latter statement by observations that the sporangial bodies of *L. Lomaxi* which are attached to a strobilus in his possession and are approximately four and one-half millimeters in length are immature rather than ripened, while those which have been shed average nearly six millimeters in length. Darrah believes that he is entirely within the bounds of the genus *Lepidocarpon* in his assignment since these "seed bodies" are merely more mature seeds. We have no basis for questioning his conclusions.

It should be pointed out, however, that this species, *L. glabrum*, which is shed free of the sporophyll upon maturity, does not conform to one of the major characteristics of the genus as recognized by Scott and already pointed out above, i.e., "when mature the megasporangium of *Lepidocarpon* is enclosed by an integument — growing up from the tissue of the sporophyll" and the "sporophyll, together with the integumented megasporangium and its contents, is detached entire from the axis of the strobilus."

Arnold (1938) has described as *Lepidostrobus braidwoodensis*, a lepidophyte strobilus from Braidwood, Illinois, having large megasporangia, each containing a single functional megaspore about two millimeters in largest diameter. Appressed to the triradiate apex of this spore are three non-functional

megaspores measuring about one-half millimeter in diameter. There are no investing laminae. He assigns these megaspores to the *Lagenicula* group of the form genus *Triletes*. Spores of the *Lagenicula* group are generally conceded to be of uncertain affinity, but some have been assigned to species of *Lepidostrobus*. Arnold believes these spores to be indicative of the distinct evolutionary trend among the Paleozoic lycopods in the reduction in number of functional spores and the increase in the size of the functional one. He recognizes *Lepidocarpon* as representing the highest attainment in this line.

Bocheński (1936) made a similar report on two species of *Lepidostrobus*, *L. major*, with a mature functional spore nearly a centimeter long, and *L. Bohdanowiczii*, with a smaller megaspore. In both these species the other members of the tetrad are present in the megasporangium as non-functional spores. Bocheński believes there is no integument present but records the occurrence of a likely tissue as a remnant of the prothallus. Schopf (1938A) questions this interpretation.

The occurrence of a single functional megaspore essentially filling the sporangial cavity, in association with the non-functional members of the tetrad are characteristics which agree with those given by Scott as being diagnostic and of major importance for *Lepidocarpon*. Apparently the absence of well developed lateral laminae closely investing the sporangium is considered by Bocheński to be of sufficient importance that the distinction between *Lepidostrobus* and *Lepidocarpon* may be based on their occurrence or absence. The poor state of preservation of Arnold's material makes further conjecture regarding it difficult. The much larger relative size of the non-functional spores to the functional one, than is known to occur in *Lepidocarpon*, may be considered indicative of the transitional nature of the species *Lepidostrobus braidwoodensis*. In our material, the non-functional spores have a much larger actual size but are smaller proportionally when considering the size of the functional megaspore.

It is obvious that the problem raised by the inclusion within the genus *Lepidocarpon* of *L. glabrum* Darrah in which the significance of the investing laminae is minimized, and the inclusion within the genus of *Lepidostrobus* of species which possess but a single functional megaspore, thus involving the two significant criteria of Scott's original diagnosis of *Lepidocarpon*, is one which must receive further serious consideration as to the generic limitations of these and related Paleozoic lycopodiaceous strobiloid forms.

Summary

A portion of a calcified strobilus is recorded from the Des Moines series of Iowa and is here described as a new species, *Lepidocarpon ioense* Hoskins and Cross.

A detailed description of the structure is correlated with the original generic designations of D. H. Scott.

A review of some recently described species of Paleozoic lycopodiaceous strobili suggests the need for further consideration of the generic limitation of *Lepidocarpon* and allied genera.

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Notes on the Lepidocarpaceae[1]

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Introduction

Members of the Lepidocarpaceae are characteristic of the Eur-American floral province and are known to be present in both the Lower and Upper Carboniferous. Both in western Europe and in America recent records have added to our knowledge of this plant family, and it is now possible to present a discusison of the classification and evolution of the groups included in the lepidocarp alliance. It is the purpose of this paper to call attention to some of the bio-characters[2] which appear to be important in distinguishing lepidocarp genera but which have not been given equal consideration by different authors, thereby leading to some ambiguities and conflicting conclusions. It is hoped that this review will lead to greater consistency of treatment and to more rapid progress in understanding the geological and biological history of this group of plants.

The writer wishes to acknowledge the help of Dr. J. Marvin Weller and thank him for critically reading the manuscript.

The Lepidocarp Family

The Lepidocarpaceae, like many other families of fossil plants, represent a group of indefinite taxonomic status. This family seems never to have been formally diagnosed, and hence its taxonomic validity has not been established beyond question — rather it has been a name defined through implications lent by the genera included in it. In the writer's opinion it comprises a group having undoubted natural affinity whose scope seems to be comparable to certain families of modern plants. The Lepidocarpaceae can be defined briefly as follows:

Ligulate lycopsid plants, of arboreous or arborescent habit, producing male and female fructifications separately (probably never in the same cone, nor in juxtaposition on fertile branches equivalent to cones). Female fructifications specialized so that individual sporophylls or parts of them have assumed the essential characters of seeds in each of which only one megaspore normally matures. Sporangium indehiscent in the sense that the seed megaspore is not expelled; seed megaspore exceedingly large and lacking the thick impervious type of spore coat that characterizes the megaspores of free-sporing lycopsids.

A rather sharp distinction should be made between the lepidocarp family

1 Published by permission of the Chief, Illinois State Geological Survey.

2 A bio-character is considered to be a definable unitary feature that has hereditary significance.

(Lepidocarpaceae) and the other groups of Paleozoic lycopsids because the differences between lepidocarp fructifications and fructifications of all the free-sporing lycopsids appear to be valid criteria for at least family differentiation. The foregoing diagnosis of this family is, nevertheless, incomplete because definite knowledge of the vegetative characters is still lacking. It is hardly conceivable that the vegetative organs are wholly unrecognized in the fossil flora, but they are probably classified erroneously at present in some other family.

The writer suspects that plants classified as *Lepidophloios* Sternberg[3] may be vegetative correlatives of genera belonging in the Lepidocarpaceae. *Lepidophloios scoticus* Kidston is the only species of this genus whose fructification characters have been even partially ascertained. Its cones are borne on specialized branches, an advanced mode of fructification *not* characteristic of *Lepidostrobus* or lepidodendrids in general. Nothing whatever is known, however, of the spores produced by these cones. *L. scoticus* is restricted to the Lower Carboniferous, the cones being known from oil shales of the Calciferous Sandstone series in Scotland. At other localities and horizons the only evidence as to *Lepidophloios* fructifications still has to be deduced from association of disconnected fruiting structures. The lepidocarps, although they generally have passed unrecognized, appear to be among these associated types. In America *Lepidophloios* seems to be the only well represented group of lycopsids whose mode of fructification is so obscure. The lepidocarps, on the other hand, do not seem to have as plausible affinities with any other group based on vegetative characters.

The fact that the Lepidocarpacaceae and *Lepidophloios* coincide in their time range, both being limited to the Carboniferous and both being reasonably well represented throughout these beds, is perhaps as definite a point of evidence as can be cited now. *Lepidophloios* aff. *L. laricinus* (Sternb.) Sternberg is a characteristic species found in roof shales over the Herrin (No. 6) coal which, in addition to the Mazon horizon, has also provided specimens assigned to *Lepidocarpon mazonense* Schopf. A form identified by Lesquereux as *Lepidophyllum auriculatum* (probably *Lepidocarpon*), was found at St. John (Perry County, Illinois, above No. 6 coal) closely associated with a species of *Lepidophloios* which Lesquereux (1870, p. 432, 439; 1880, p. 422, 450) identified by the same specific name. He considered that the two species probably were correlated. *Lepidophloios* ranges through the English Lanarkian (which includes the "Lower Coal Measures") and is characteristic of the Lower Carboniferous where it is associated with *Lepidocarpon* (Walton 1935; Walton, Wier & Leitsch 1938). Other occurrences need not be cited here but the apparent association of these fossils may be significant.

Correspondence that passed between the late Professor A. C. Noé and W. Hemingway of Derbyshire, England, concerning a shipment of sections sent

3 Sternberg's original spelling of this name was "Lepidofloyos." There is a question whether the original spelling, or the now accepted "correction" of it should be used. I am indebted to Dr. F. C. MacKnight for calling this to my attention.

Prof. Noé in 1925 contains a significant statement regarding the relations between *Lepidophloios* and *Lepidocarpon*. Mr. Hemingway wrote:

> *Lepidocarpon "Lomaxi"* represents quite a group of seed-like bodies and cannot yet be separated in sections. *Lepidocarpon majus* [n. comb.!] has been found attached to stems of *Lepidophloios laricinus* and *Lepidocarpon lanceolatum* [n. comb.] to *Lepidophloios acerosus*. They are therefore the megasporocarps of *Lepidophloios*.

Mr. Hemingway also stated:

> *Lepidocarpon Lomaxi* represents the "seed" of *Lepidophloios*—they have been found attached. The so-called species probably represents the seeds of several species of *Lepidophloios*. *Lepidostrobus Oldhamius* also represents the microspore cones of *Lepidophloios* and embraces several species.

It may be that Mr. Hemingway had reference to the leaves at the tip of a vegetative branch of *L. acerosus* (L. & H.) Kidston (instead of "*L. laricinus*") that Kidston (1893, pp. 553, 559) illustrated and compared with *Lepidophyllum majus* Brongniart, and to the lanceolate leaves Macfarlane (1883) associated with *Lepidophloios laricinus* (=*scoticus* Kidston). If so, these associations perhaps have value only as analogies. Mr. Hemingway, however, has evidently also noted the lepidocarp characters commonly associated with the *majus* type sporophyll, and others which supported an identification with *Lepidocarpon lomaxi*.

A few obvious lines of investigation suggest themselves for obtaining additional evidence. To judge by the earlier papers of Kidston and others the cones of *Lepidophloios scoticus* are not rare. Even though they all may be immature when intact, evidence of the spores should be obtainable from them upon maceration. An attempt should be made to obtain compression specimens of *Lepidocarpon* from the Calciferous Sandstone series where they are to be expected because of their common occurrence as petrifactions. Mr. Hemingway's suggestion that *Lepidocarpon lomaxi* is separable into more definite species deserves consideration, and if the *lomaxi* group is reinvestigated, evidence bearing on the relationship of *Lepidophloios* also should be sought. It is particularly important that the geological longevity of respective diagnostic biocharacters distinguishing the various intimately related species be investigated.

If the suggested correlation of the genus *Lepidophloios* with several lepidocarpaceous genera be eventually substantiated it need occasion no great surprise. In the main it may be taken to indicate that in this Carboniferous group, as in modern plant groups, reproductive organs in general are more responsive to evolutionary change than are the vegetative ones.

The oldest members of the lepidocarp family have been reported from the Calciferous Sandstone series of the Lower Carboniferous (Scott, 1900, 1901; also reported from Arran by Walton 1935, p. 318), and *Cystosporites* appears among the youngest members reported in Stephanian beds of Lower Silesia and the Saar district (recorded as *Triletes giganteus;* Zerndt, 1937, 1940). The family is well represented in America both in beds of Pottsville and Allegheny age. *Lepidocarpon* also has been reported from Calhoun coal balls (Fisher and Noé, 1939) of probable upper Conemaugh age (cf. Schopf, 1941). Diversification seems more apparent within this family in America than in the old

world. This may be explained, in part at least, by the fact that the best fossiliferous (coal ball) deposits in America are younger than those most studied in Europe, and these younger beds may contain representatives of the family at the apex of its geologic history.

The Genus Lepidocarpon

Lepidocarpon Scott, first recognized and defined about forty years ago, is the type genus of the Lepidocarpaceae. Scott's original diagnosis (Scott 1900, p. 309) is as follows:

> *Lepidocarpon*, gen. nov.—
>
> Strobilus, with the character of *Lepidostrobus*, but microsporangia and megasporangia each surrounded by an integument, growing up from the upper surface of the sporophyll. Megasporangium completely enclosed in the integument, except for a slit-like micropyle along the top. A single functional megaspore developed in each megasporangium. Sporophyll, together with the integumented megasporangium, detached entire from the strobilus, the whole forming a closed, seed-like, reproductive body.
>
> It is proposed to name the coal measures form *Lepidocarpon Lomaxi* and that from Burntisland *L. Wildianum*. Both were included by Williamson under his *Cardiocarpon anomalum*, which however, is quite different from the seed so named by Carruthers.

Scott also noted on page 307 that "the outer layer of the sporangial wall has the columnar or palisade-like structure characteristic of *Lepidostrobus;* it is lined by a more delicate inner layer which may be several cells thick."

In the diagnosis published with his more complete treatment of *Lepidocarpon* (1901), Scott omitted mention of the microsporangiate structures because he was more doubtful of their relationship than he had been previously. The main points of his later diagnosis are as follows:

(1) Strobilar habit—like *Lepidostrobus;*
(2) Integuments present when mature;
(3) Megasporangium entirely enclosed except for micropylar slit;
(4) A single functional seed megaspore nearly fills the sporangial cavity;
(5) Sporophyll became detached from the cone axis as a unit.

To these an additional point may be added from p. 304 of Scott's detailed description.

> The structure of the sporangium is however the same, as in its naked condition [e.g., in *Lepidostrobus*]. The wall has a superficial columnar layer, with a more delicate lining tissue within it. The cells of the columnar layer are often shorter and broader than in the non-integumented sporangium [of *Lepidoacrpon lomaxi*] owing no doubt to superficial extension of the wall; at other places, however, and especially at the apex where the narrow ridge of the sporangium fits into the micropylar opening, the structure is quite unchanged.

In defining *Lepidocarpon* the writer considers it advisable to follow Scott's generic interpretation rather carefully. The diagnosis provided by Scott in 1900 and slightly emended in 1901 may well be altered, however, so that it will reflect some of the additional observations made by various workers during the last forty years of sporadic study of this group of plants. It is now possible to refer compression and impression specimens to this genus and with the progressive elimination of non-biologic differences (resulting from differences of pres-

ervation) the classification of these fossil plants becomes more truly phyletic. Lack of diagnostic information due to vagaries of preservation will probably always make it necessary to recognize non-biological distinctions to some extent in scientific classification. *Lepidocarpon*, however, appears to be an example where these differences can be relegated to less than generic importance.

Lepidocarpon Scott (1900)

(Revised diagnosis)

A genus of ligulate lycopsid plants characterized by,

(1) *Strobilar habit of fructification;*
(2) *Sporophylls attached to cone axis as in Lepidostrobus;*
(3) *Sporophylls shed entire by disintegration of the cone axis;*
(4) *Seeds provided with a distinct integumentary organ;*
(5) *Integument, attached lateral to sporangium along pedicel, invests the sporangium closely and its two edges project ventrally above the seed body as a micropylar crest;*
(6) *Slit between the two membranes of the crest corresponding morphologically to a micropyle;*
(7) *Megasporangium large, indehiscent (fertile spore not shed), attached for the greater part of its length to the ventral midline of the pedicel;*
(8) *Outer wall of sporangium of prismatic or columnar cells, similar in structure to the sporangium wall of free-sporing lycopods;*
(9) *Intrasporangial tissue more persistent than in most free-sporing lycopsids;*
(10) *Seed megaspore relatively enormous (for lycopsids), spore coat with more or less fibrous texture and trilete apparatus at its proximal end (usually turned toward the anterior or distal end of the seed);*
(11) *Maturation of only one seed megaspore per sporophyll, derived from a single tetrad; abortive megaspores also evident.*

English Species of Lepidocarpon

The cone of the genotype species, *Lepidocarpon lomaxi* Scott, is medium sized (20-30 mm. diameter), of compact structure with sporophyll laminae long and strongly reflexed upwards. Toward the tip of each lamina the blade seems to have been membranous and impersistent but near the seed it was rather fleshy and is commonly well preserved. Mature seeds are fully integumented but the integument is frequently incomplete on immature specimens, and in this condition it is represented by fleshy cushions along both sides of the pedicel. The integument is presumed to have been formed last, late in ontogeny. A simple layer of columnar or prismatic cells, very similar to the prismatic layer of *Lepidostrobus*, covers the sporangium. Radial length of fruit is 8-14 mm., — tangential height through seed body 5-11 mm., — width at distal end of seed body 5-12 mm. This species occurs in the English "Lower Coal Measures." It has been reported in most coal seams of this age that have provided coal balls, and thus it must be considered a rather widespread and characteristic element of the upper Lanarkian flora.

Scott also described a second much older species, *L. wildianum*, from the Calciferous Sandstone at Pettycur that is somewhat smaller than *L. lomaxi*, but otherwise not readily distinguishable. The seed megaspore shows an "irregular reticulation" (Scott, 1901, p. 315) which in all likelihood is similar to the fibrous network composing the *Cystosporites* membrane. *L. wildianum* is doubtless a distinct species, and future studies will probably make known biological

characters by which it can be recognized, but at present its true distinguishing characters are not known. More thorough examination of Lanarkian forms will probably also result in additional species being recognized, as suggested by Scott and others who have examined many "Lower Coal Measures" specimens.

For convenience *L. lomaxi, L. wildianum,* and closely related but as yet undistinguished forms of Lower Carboniferous and Lanarkian age will be referred to as the *lomaxi group.* Because they possess certain characteristics reminiscent of those of free-sporing lycopsids and, in addition, because of their antecedent stratigraphic position relative to the American species, they are regarded as examples of the more primitive lepidocarp stock.

In 1914 Kidston described *Lepidocarpon westphalicum* from the Yorkian age ironstone deposits near Dudley. The type consists of an axis with scars of sporophylls previously shed and a central portion on which parts of about twenty attached sporophylls are visible. The cone is of compact construction and is preserved without crushing, but only surface features were observed and these are not all that might be desired The laminae may be of moderate length and appressed to the cone, judging from Kidston's Figs. 1, 3, 4, and 5, where they seem to appear in lengthwise fracture on both sides of the specimen. Kidston states that the "whole of the bracts have disappeared" and so the laminae, apparently seen, may be illusory. The laminae, however, may have been membranaceous distally, similar to those of *L. lomaxi* described by Scott. The particular feature that decided Kidston on the generic identification of this species was the sporangial integument, but he did not note a micropylar slit. So far as known the integument appears generally similar to that of *L. lomaxi.* Most of the sporangia have their disal ends exposed, and on many of these a small terminal irregularity appears which should be opposite the trilete apparatus of the seed megaspores inside them.[4] No remnants of the seed megaspores have been reported in *Lepidocarpon westphalicum* although they may be present. There are no very definite biological characters distinguishing *L. westphalicum* from members of the *lomaxi* group except for differences in size. The cone is about 15 mm. in diameter in contrast to 20-30 mm. for *L. lomaxi;* the sporangia are smaller and have a height-breadth ratio of 2½ to 1 whereas in *L. lomaxi* the ratio is slightly less than 2 to 1.

Records of American Lepidocarpaceae

Lepidocarpon was first reported in America by Noé (1931) in a list compiled from investigations by certain of his students. A discussion of this material was included in Miss Krick's (1932) report on seed-like fructifications from the Harrisburg (No.5) coal in Illinois. Later Fredda Reed (1936) described other isolated Lepidocarp sporophylls from the same source. The presumptive evidence that these specimens belong to *Lepidocarpon* is good, but it can not be considered entirely conclusive because the manner of pedicel

4 These may be the "smooth pits at the basal end" which Darrah (1941, p. 87) refers to as sporangial attachment marks but this interpretation is not indicated by Kidston's discussion.

attachment was not demonstrated in either case. The importance of such attachment was not then realized, and it is probable that the specimens studied by both of these authors were attached to a cone axis in the true *Lepidocarpon* fashion. Miss Reed has recently demonstrated such attachment for other Harrisburg specimens by means of an adequate series of tangential slices described at the 1939 meeting of the Paleobotanical Section. The importance of pedicel attachment in the lepidocarps is emphasized below in connection with the discussion of *Illiniocarpon*.

Both Noé and Krick identified their lepidocarp material as *Lepidocarpon lomaxi* Scott. This specific identification is doubtful, however, because the similarities mentioned by Krick concern chiefly the size of the seed body. Without supporting evidence this cannot be regarded as positive proof of specific identity. The histological details particularly must also be carefully considered. The Harrisburg material appears to be significantly younger than the "Lower Coal Measures" specimens studied by Scott.

The sporophylls described by Fredda Reed (1936) were not specifically identified. They appear to correspond with immature and abortive megasporangia such as Scott reported for *L. lomaxi*. However, the sporangium wall had a sclerotic rather than a prismatic external layer of cells. This may be a feature of considerable significance in lepidocarp evolution, inasmuch as it indicates the loss of a primitive character well represented in the lomaxi group.

The writer described two new species belonging to the Lepidocarpaceae in 1938 (Schopf, 1938a). One *(L. mazonense)* is a form common in the Mazon concretions above the Colchester (No. 2) coal in Grundy and Will counties which resembles in many respects the generalized type traditionally known as *Lepidophyllum majus*. Its reference to *Lepidocarpon* was definitely established although it is not certain that this species is distinct from earlier described but less adequately understood forms. *Lepidophyllum majus* itself is confused taxonomically because the type is a poor specimen with the seed body missing; it was originally designated *Filicites (Glossopteris) dubius* by Brongniart (1822), and its name was later changed in the Prodrome (1828, p. 87). It would probably be impossible to prove that the Mazon form is cospecific with the type, even if such were actually the case. Certainly some of the specimens referred to *L. majus* are *not* cospecific with *Lepidocarpon mazonense*, although there is no reason for believing them to be generically distinct. Probably Brongniart's species will pass into disuse because of the inconclusive nature of its type and the consequent doubt as to its accurate specific definition.

A brief description of a new type of lepidocarp seed was presented in the same publication (Schopf, 1938a). This differs significantly from the genus *Lepidocarpon* and a new generic name, *Illiniocarpon*, was given it. In transverse sections through certain parts of the seed body it closely resembles *Lepidocarpon*, but a qualitative and diagnostic difference appears in the manner of sporophyll attachment to the fertile branch. This distinction is commonly shown in longitudinal sections, and single transverse sections of either *Lepidocarpon* or *Illiniocarpon* cannot be counted on to provide conclusive evidence of

the distinction between the two genera. The individual sporophylls (not cones) of *Illiniocarpon* are properly described as *pedunculate*, and by modification of the pedicel and other changes these plants have lost the strobilar habit of fructification to a significant degree. The integumentary organ (which, as Scott emphasized, is *not* merely the upturned margin of sporophyll lamina) is more specialized, and the actual lamina is extended, broad, and doubtless served as a wing for dispersal of the fruit after it had been shed as a unit from the fertile branch. The laminae of some *Lepidocarpon* species also probably served this same function [e.g., *L. mazonense*, (?) *L. linearifolium* (Bassler)] and this may perhaps be regarded as a minor example of evolutionary parallelism in the two groups.

Numerous large fibrous sack-like bodies (seed megaspores) with trilete appartus at one end similar to those Zerndt (1930) described as *Triletes giganteus* have been obtained by the writer from maceration residues of coal. These seed megaspores are closely related to *Lepidocarpon mazonense* but because essential diagnostic characters can not be established and because these isolated seed megaspores appeared to be moderately generalized, it has seemed unwarranted to identify them with either of the two genera that had been previously recognized in the Lepidocarpaceae. Their characters, however, fully supported their reference to this family, and the genus *Cystosporites* was proposed for their reception (Schopf, 1938b). This genus may be entirely or only in part equivalent to the Lepidocarpaceae but it clearly exceeds the scope of other genera more adequately diagnosed on the basis of their sporophyll structure. Biologically it appears to overlap both of the established genera, and the isolated spores are thus classifiable with less precision than is possible where complete fruits are available, but for scientific reporting a name is none the less essential for them. It is incorrect to assume that *Cystoporites* is only the seed megaspore of *Lepidocarpon* (Darrah 1941, p. 89), because its relationship is definitely broader. The significant contribution afforded by the recognition of *Cystosporites* is that it shows best how geologically long lived and widespread the Lepidocarpaceae were in Carboniferous times (cf. Schopf 1938b; Zerndt, 1937, p. 68; 1940, p. 142). Not only is *Cystoporites* a practical generic designation of use in classification of these isolated seed megaspores, but it also indicates a group of natural affinity and certain biological significance. The delimitation of its natural affinity is in fact far more precise than a great many other generic groups commonly used in the classification of fossil plants. It should be recognized that the introduction of such a genus is not a "purely artificial method of classification" and that plants which have been classified as *Cystosporites* do not already possess any other properly assignable generic names.

In 1938 the writer discovered that the holotype of *Carpolithes corticosus* Lesquereux is clearly cospecific with a form previously discovered in the Mazon shale which he had interpreted as a variant of *L. mazonense*. Further study showed conclusively that Lesquereux' species was quite distinct from *L. mazonense*. Later, when Janssen's treatise on certain of the Lesquereux types was in preparation, the writer was invited to contribute a revision of this form,

and the species was transferred to the genus *Lepidocarpon* (Schopf, in Janssen, 1940). *Lepidocarpon corticosum* (Lesq.) Schopf is most closely related to *L. novaculeatum* and *L. robustum* both of which were transferred from Bassler's genus *Cantheliophorus*[5] which is discussed on a later page. An abortive megaspore from the original tetrad is present in its normal position near the anterior of the seed body in the holotype of *L. corticosum* in addition to the large fertile one. *L. mazonense* and *L. corticosum* furnish substantial proof that histological features are not essential for recognition of this genus, and in this respect Kidston's generic identification of *L. westphalicum* is confirmed.

Darrah has recently described a new species under the name of *Lepidocarpon glabrum* (1941). Although cellular detail is preserved in his specimen few characters were available for distinguishing this species and consequently its generic classification deserves more critical examination. This plant has seeds which consist (so far as the types at least are concerned) of a sporangium with well developed internal tissue surrounding the seed megaspore. No information as to the pedicel, lamina, or axial attachment of the complete sporophyll is provided nor is there any evidence of the integuments that characterize mature seeds of all other members of the genus.[6]

Illiniocarpon was distinguished from *Lepidocarpon* (1) because the sporophyll was pedunculate in one and normally situated on a strobilar axis in the other; (2) because in *Illiniocarpon* the integuments are separately vascularized posterior from the peduncle and are developed differently, being far more evaginate; (3) the sporophyll lamina in *Illiniocarpon* is straight and not reflexed as in *Lepidocarpon*. (4) Apparently correlated with this last character is a further specialization of the sporangium wall near the ligular region at the anterior end of the seed which has not yet been found in *Lepidocarpon*.

Lepidocarpon glabrum is inadequately known regarding (1) strobilar (compact, lax) or non-strobilar habit, (2) presence, absence, or nature of the true lepidocarp integument, and (3) character of the lamina. It cannot be positively identified with *Lepidocarpon* because these important diagnostic characters

5 The writer is not quite certain, that Bassler's *L. robustum* and *L. novaculeatum* are specifically distinct from each other or from *L. corticosum*. The relationship in any case is evidently very close. However there seems to be ample basis for specific discrimination between the other forms Bassler described. Nevertheless, the arrangement of plates and descriptive data is such that careful study of Bassler's paper is required in order to clearly establish the specific differences.

6 Darrah has described the external layer of the sporangial wall as the "integument." From a purely descriptive standpoint the term may be so used, but it is inadvisable because all other Lepidocarps have a distinct organ, called the *integument* by most writers, that is entirely separate from the megasporangium. Specimens of *Lepidocarpon glabrum*, do not now possess any integument of this sort. Whether the sporangia were originally integumented when the sporophyll was complete is unknown, although from Darrah's account it seems unlikely that they were.

Darrah also infers (op. cit. p. 95) that the sporangial wall of *Lepidocarpon* includes sclerotic "protective tissues." Scott's description of specimens of the *lomaxi* group do not support this conclusion and in only one form (aside from *L. glabrum*) has sporangial wall sclerenchyma appeared (Reed, 1936).

have not been observed. Characters other than those of the seed megaspores are shown, however, so that the species is classifiable with more precision than is possible when only isolated seed megaspores are present. Positive differences are exhibited which may have significance of more than specific value. The seeds of *L. glabrum* are mature, and the individual sporangia (evidently *not entire sporophylls*) have been shed. There is no previously described species of recognized lepidocarps in which shedding of mature sporangia apart from their integument was possible. The number of isolated sporangia which Darrah records indicates decisively that shedding of the individual sporangia was a normal occurrence in this species. The only mark reported on the mature sporangial seed (which in this species is equivalent only to a ripened ovule — without the additional sporophyll parts possessed by seeds of other lepidocarps) is at the point of its attachment to a pedicel or pedicel-equivalent. Mature megasporangia (seeds) of *Lepidocarpon* or *Illiniocarpon* were not so separated from their sclerous integuments. Abortive and immature sporophylls of *L. lomaxi* commonly lack the integument, but *functional* seeds are equipped with them. Typical *Lepidocarpon* sporangia are not sclerotic but have walls whose prismatic layer is strikingly similar to that of *Lepidostrobus*. Their preservation appears primarily to result from the efficient protection of the integumentary organ.

Darrah's illustrations and description of the wall of *L. glabrum* sporangia (seeds) thus suggest that they differ considerably from sporangia of the *lomaxi* group. The unintegumented sporophylls described by Fredda Reed also are noteworthy in their lack of a prismatic sporangial coat. Similar sporangia of the *lomaxi* group described by Scott possess a somewhat thicker sporangial wall tissue than the integumented forms, but the prismatic layer apparently is developed typically in all. *Illiniocarpon* shows a different type of modification in the sporangial wall. In the lower anterior region the wall is thick, and although the prismatic layer is easily recognized it is considerably modified and possesses larger cells with undulant walls (cf. Fig. 9; Schopf, 1938a). The anterior prongs show rather typical prismatic (columnar) structure but the posterior part of the sporangium wall is more delicate and can hardly be considered prismatic. In fact it resembles the epidermal layer of a well protected ovule. This is what would be expected if the lepidocarp sporangium were modified in accordance with the degree of exposure and protection afforded by the integument. The adaxial ("posterior") part of the seed body in *Illiniocarpon* is well enclosed and probably was somewhat better protected than in *Lepidocarpon*, but the anterior part of the seed (facing the lamina) may have been more exposed because the sporophyll lamina was not reflexed upwards around it. Evidently the character of the sporangium wall deserves more thorough study in the lepidocarps because it probably reflects the type of seminal modification.

Intrasporangial tissue within the dermal layer in *Lepidocarpon glabrum* also appears to be a significant character. In the unintegumented sporangia of the *lomaxi* group the sporangial tissue is consistently thicker than in the integumented seeds, and this was explained on physiological-ecological grounds. In

L. glabrum, however, this tissue is so much more developed that the character has probably become hereditary. Concordantly the seed megaspore of *L. glabrum* also occupies proportionally less space in the sporangium than in those of other lepidocarps. This appears to be true, at least in so far as the sections shown on Darrah's Plate II are typical of the species. In the *lomaxi* group and in *Illiniocarpon* there is no comparable development of the "nutritive" tissue.

Darrah's species therefore probably lacks diagnostic features which assuredly would place it in the genus *Lepidocarpon* and in addition shows other modifications which indicate considerable divergence from that group. Because of the lack of a prismatic palisade layer, Fredda Reed's specimens may occupy an intermediate position between *Lepidocarpon* Scott and Darrah's divergent type, *L. glabrum*. It is important that the divergent characters of the latter be recognized, and the writer regards them, in conjunction with the lack of information in other particulars, as conclusively indicating a need for *L. glabrum*, at least, being classified under a distinct generic name. However, there is no basis for doubting that its relationship is definitely with the Lepidocarpaceae.

Darrah's comparison of *Lepidocarpon glabrum* with *Lepidocystis* is highly significant, and it may be that this ambiguous and poorly defined group will be clad with useful biological meaning after all. The *Lepidocarpon* described by Reed from Harrisburg coal balls, which also lacks a prismatic sporangial wall, is not integumented and may not be abnormal as Reed supposed. It also might be classified with this divergent lepidocarp group having "lepidocystoid" characters. However, there appears to be considerable disharmony among specimens which have been labeled "*Lepidocystis*" in the past. Few of them have been shown to possess spores in place, but those specimens in which spores have been recognized are clearly referable to the free-sporing lycopods, probably to the Lepidodendraceae. It is altogether possible (in fact, probable, in view of *L. glabrum*) that many specimens which do not appear to have spores, actually enclose unrecognized seed megaspores of the cystosporean type. These specimens would necessarily belong in the Lepidocarpaceae. The availability of the name *Lepidocystis* for lepidocarp species with this latter character evidently must be determined by restudy of the genotype which is *Lepidocystis pectinatus* Lesquereux.[7]

The conclusion that there are at least two divergent branches of the primitive integumented lepidocarp stock in the American Pennsylvanian is plausible. One branch shows greater specialization of the integuments and other structures and is represented by *Illiniocarpon*. The other branch is represented by *L. glabrum* in which the seeds have been subject to a different kind of specialization involving, probably, loss of the integument. Presumably the less specialized true *Lepidocarpon* type coexisted with both of the more specialized lineages, but the ancestry of the latter groups may be sought among the more primitive lepidocarps that geologically antedate them.

7 The holotype of this species is listed in Lesquereux' "Coal Flora" as No. 423 of the Lacoe collection, now in the U. S. National Museum at Washington, D.C.

Cantheliophorus and Lepidocarpon

A substantial addition to the Lepidocarpaceae was made by Harvey Bassler (1919) in his description of twelve species under the generic name of *Cantheliophorus*, although he misinterpreted the structure of his material.[8] Bassler recognized that his species were highly specialized and his statement (1919, p. 97) that "members of a group with structure as intricate and diverse as this will have high stratigraphic value if treated with great systematic refinement" seems more than ever warranted.

Lepidocarp sporophylls in shale are preserved differently, depending upon whether the plane of rest is determined by a broad lamina or by the form of the seed body itself. The seed body generally is higher than broad, and if the lamina forms too narrow an appendage, the height of the seed body is most likely to parallel the bedding. All of Basser's species seem to have been preserved in this position and those he illustrates are compressed parallel to the organic longitudinal plane. Thus they appear much different from most specimens of *Lepidostrobophyllum* in which the laminal breadth more consistently parallels the bedding planes. Although characters of size and proportion of sporophyll laminae are generally considered to be of specific importance, they probably lack generic significance.

The features Bassler considered to be unique in *Cantheliophorus* were, (1) two sac-like sporangia per sporophyll, borne on short sporangiophoric stalks; (2) a plate of sterile sporophyll tissue ascending from the ventral midline of the pedicel and to which the sporangiophores were attached laterally and distally. The structures ilustrated, however, do not support this morphologic interpretation of them. They are instead more satisfactorily explained by comparison with *Lepidocarpon*, and according to this interpretation they comply entirely with the essential diagnostic characters of that genus. Bassler has not presented evidence proving the existence of two sac-like bodies on any single sporophyll — he has not shown the "median" plate to be other than the compressed form of the *Lepidocarpon* integument.

The "sporangia" of *Cantheliophorus* agree precisely with seed megaspores of the lepidocarps, and they must be interpreted in this light. It is understandable how Bassler and others failed to note this resemblance because no lepidocarp megaspores had been isolated previously and they are remarkable objects quite different from the common free-sporing forms in general outline and size. Nevertheless the *single* fertile lepidocarp seed megaspore is clearly recognizable from Bassler's figures for most of the *Cantheliophorus* species. They agree in habit with those the writer has illustrated from *Lepidocarpon corticosum* (Schopf 1938a, 1938b, 1940) and also with seed megaspores obtained from *L. mazonense*. The agreement with seed megaspores Bocheński (1936) obtained

8 Bassler's descriptions are given in terms of his hypothetical interpretation of the sporophylls, but there is no reason for preserving this terminology because his specimens are easily described by other terms that were previously and still are in good technical usage.

from lepidocarp cones in the Lower Silesian coal field is just as striking.[9]

This striking agreement is by no means limited to the seed megaspores but continues in remarkable detail to all other portions of the lepidocarp sporophylls and is perhaps best illustrated by comparison with a larger species of *Lepidocarpon* (as yet undescribed) represented by numerous examples in the Illinois Survey collections from near Wyoming Hill (Muscatine County) Iowa. The latter specimens are compressed in a dark fissile shale and thus entirely agree with Bassler's in mode of preservation, even showing similar lengthwise folding of the sporophyll laminae. Where the shale is intact these sporophylls contain well preserved lepidocarp seed megaspores. On mild macerative treatment the fibrous megaspores of cystosporean type are easily isolated; they show the characteristic trilete commissure at the apex and are associated with abortive tetrad members. The "plate" Bassler described is represented in these specimens (just as it is shown in his illustrations of *Cantheliophorus*) by a very definite micropylar crest which is similar to that unmistakably shown in *Lepidocarpon mazonense*. The coaly and external integumentary impression surfaces of Wyoming Hill shale specimens agree absolutely with Bassler's figures and characterization (*op. cit.*, p. 79) as "usually granulose to the unaided eye and minutely rugulose-bullate under the lens." Observation under the Greenough microscope shows the surface rugosity is due to the type of sclerotic cells present on integumentary surfaces. *Lepidocarpon corticosum* (Lesq.) although preserved a little differently also is similar to Bassler's material in many respects.

Such precise agreement and the absence of any conflict in generic characters indicate that species of *Cantheliophorus* Bassler must be referred to the older genus *Lepidocarpon* Scott, and this has been proposed in an earlier publication by the writer (Schopf, in Janssen, 1940). The geologic time range of *Cantheliophorus* species is entirely that of *Lepidocarpon*, and there is no reason for concluding that *Cantheliophorus* is in any biological way distinct or distinguishable from Scott's genus.

Darrah (1941, p. 89) recently has stated, that "a number of sporophylls of the *Cantheliophorus* type . . . bear many megaspores of the familiar 'Triletes' type" and on this account he does not accept the synonymic reference of *Cantheliophorus* to *Lepidocarpon*. It is difficult to understand how any sporophyll bearing numerous Triletes-type megaspores can justifiably be assigned to *Cantheliophorus* or to *Lepidocarpon*. Bassler found none in the examination of a large suite of specimens, and in failing to definitely recognize spores of any sort, concluded (*op. cit.*, p. 81) that the plants probably were homosporous. It would seem that no matter what apparent similarities there may be between the superficial form of the sporophylls, no free-sporing plant can be assigned to *Lepidocarpon* (or to *Cantheliophorus* which is in complete synony-

9 Bocheński assigned these specimens to *Lepidostrobus* and compared the spores with *Triletes giganteus* Zerndt and *Sporites varius* Wicher, but his specimens also must be identified with *Lepidocarpon*. There is a great difference between the spores he isolated from these specimens and the free-sporing *Triletes* and *Sporites* genotypes, and lepidocarp megaspores now may best be compared with *Cystosporites*, a genus which, in part, was proposed for reception of Zerndt's and Wicher's species.

my with it). The presence of free-sporing megaspores is a character which not only excludes a plant from these genera but also places it beyond the family limits of the Lepidocarpaceae.

Summary

Family characteristics of the Lepidocarpaceae are given. It is suggested that *Lepidophloios* is a possible lepidocarp representative showing the vegetative features of these plants. The diagnostic characteristics of *Lepidocarpon* are reviewed, and the generic diagnosis is rephrased. The essential distinctions Scott recognized in establishing the genus are entirely valid and should be adhered to rather closely.

The genera and species discussed include *Lepidocarpon lomaxi*, the genotype of the type genus for the family, *L. wildianum*, and *L. westphalicum*, all known from English sources. Records of *Lepidocarpon* in America are reviewed with respect to the characters used in their identification. Points which distinguish *Illiniocarpon* from *Lepidocarpon* are enumerated and the relationship of these genera with the less precisely defined genus *Cystosporites* is restated. Attention is called to divergent characteristics of *Lepidocarpon glabrum* from Iowa, and possibly also represented to a lesser degree in another lepidocarp from Harrisburg coal balls, which would seem to set them apart from the genus *Lepidocarpon*. Reasons are given for referring the American forms named *Cantheliophorus* to *Lepidocarpon*.

American lepidocarps in particular are worthy of intensive study because the diversified forms present a particularly interesting problem of plant evolution. In the following tabulation of the Lepidocarpaceae each species is listed according to its approximate age. The larger number of forms occurring in post-Pottsville beds supports the conclusion that diversification was more rapid during that time.

Post-Pottsville (Post-Westphalian B)

Lepidocarpon mazonense Schopf
L. corticosum (Lesq.)
L. novaculeatum (Bassler)
L. robustum (Bassler)
L. subulatum (Bassler)
L. linearifolium (Lesq.)
L. sicatum (Bassler)—
(also in upper Pottsville)
Illiniocarpon cadyi Schopf
Cystosporites breretonensis Schopf
C. giganteus (Zerndt)
Lepidocarpon lomaxi (?)
(Noé, Krick, Fisher & Noé)
L. sp. Reed
L. (?) *glabrum* Darrah

Pottsville
(Mid-Lanarkian to Staffordian; Mid-Namurian to Westphalian C)

Lepidocarpon westphalicum Kidston
L. lomaxi Scott
L. waldenburgense (Potonié)
Cystosporites giganteus (Zerndt)
Lepidocarpon grande (Bassler)
L. ensiferum (Bassler)
L. pugiatum (Bassler)
L. iowense Hoskins & Cross
(of Pottsville age*)

* For description see Amer. Midl. Nat. **25**(3):543, 1941. (Horizon information fide Cross June 9, 1941.)

Lower Carboniferous (Mississippian, in part)

Lepidocarpon mirabile (Nathorst) *Lepidocarpon riparium* (Nathorst)
Lepidocarpon wildianum Scott—(Calciferous Sandstone).

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Forest Invasion and Succession on the Basins of Two Catastrophically Drained Lakes in Northern Minnesota[1]

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Recently, the catastropic partial drainage of two northern Minnesota lakes, Bass Lake in St. Louis County, and Sunken Lake in Itasca County, has made possible a direct study of plant invasion and succession on soils varying from glacial drift to soils almost entirely of organic origin. The purpose of the present paper is to record the history of these two catastrophic events and to present a generalized picture of the present flora and the observed vegetational trends on the newly formed habitats. The writers first visited these localities in the fall of 1934. At this time permanent quadrats and transects were established. They were revisited by Moyle in September, 1936, and by Nielsen in September, 1939.

The historical and field data for Bass and Sunken Lakes are presented as separate sections in this paper. A general discussion of the vegetational trends as observed on the drained basins of both lakes concludes the paper. It should be pointed out that although Bass Lake and Sunken Lake both are in the northern coniferous forest region and have had a remarkably similar recent physiographic history, certain of the areas exposed and made available for plant invasion in the two lake basins are quite different. These differences are associated with the geology of the surrounding regions. Sunken Lake is a typical morainic lake of the eutrophic type, while Bass Lake is an elongate rock basin lake of the oligotrophic type.

The Vegetation of the Region

Both Bass and Sunken Lakes lie within the boundaries of the northern coniferous forest. The common upland forest trees are *Pinus resinosa, P. Banksiana, P. Strobus, Picea canadensis, Abies balsamea, Betula papyrifera, Populus tremuloides, P. balsamifera,* and *Quercus borealis* and its variety *maxima. Tilia americana, Acer sacharrum,* and *Quercus macrocarpa* occur locally on the heavier soils. Commonly associated with these upland forest trees are the shrubs *Diervilla Lonicera, Corylus americana, C. rostrata, Alnus crispa, Rubus strigosus, Vaccinium pennsylvanicum, V. caespitosum, Salix humilis, Rosa blanda, R. acicularis,* and several species of *Amelanchier.* On

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low ground, especially in bogs, the common trees are *Picea mariana, Thuja occidentalis,* and *Larix laricina.* The shrubs that are usually associated with these trees are *Alnus incana, Vaccinium canadense, Ledum groenlandicum, Chamaedaphne calyculata, Andromeda glaucophylla, Myrica Gale, Betula pumila* var. *glandulifera,* and several species of willows.

Because of extensive logging operations and numerous forest fires during the last 50 years, the original aspect and composition of the upland forest has been considerably altered. Over large areas the original white and Norway pine stands have been replaced by jack pine, aspen, and white birch.

Bass Lake

Location, Physiography, and Recent History

Bass Lake and Low Lake, into which Bass Lake drains, are located about 4 miles north of Ely, St. Louis County, Minnesota, Secs. 1-4, 9-10; T63N; R12W. Both lakes lie in the same structural basin, gouged out of the underlying pre-Cambrian crystalline rock during Pleistocene times. The present undulating topography of the region is the result of the uneven deposition of the Fourth Wisconsin (Patrician) drift and the out-cropping pre-Cambrian rock formations (Fig. 1). The physiographic relationship of these lakes to the surrounding region has already been reported by Winchell (1899), Leverett and Sardeson (1932), and Grout (1936).

The following news item, here quoted in part, appeared in the "Ely Miner" on May 15, 1925 (Anonymous, 1925):

> Bass Lake, made famous years ago by Alason Johnson who conducted a summer resort and fishing headquarters thereon, has entirely disappeared off the map and nothing now remains but a barren hole where formerly this handsome body of water was located.
>
> Adolph Dolinsek, who with a crew of six men is cutting portage between the several lakes in that vicinity, brought in the news accompanied by pictures, of the transformation. The pictures show the ground where the lake was and the cut between Bass and Low Lakes through which the water escaped from Bass into Low and thence north into international waters. . . .

Copies of some of the pictures referred to in this news item are shown in Figures 2 and 3. Examination of these pictures shows that Bass Lake was not entirely drained as stated in the news item.

Thiel (1932a, 1932b) has outlined the post-Pleistocene history of Bass and Low Lakes, the recent events leading to the catastrophic partial drainage of Bass Lake, and the nature of the glacio-lacustrine sediments associated with these lakes.

The pertinent facts presented by Thiel which are of botanical significance to this study are briefly summarized in the following statements: Bass Lake and Low Lake were esparated until recently by a ridge of glacial gravel which served as a dam between them. Seepage around a sluiceway built and used during logging operations for delivering logs into Low Lake eventually caused the gravel ridge between the lakes to give way. As a result, Bass Lake lowered

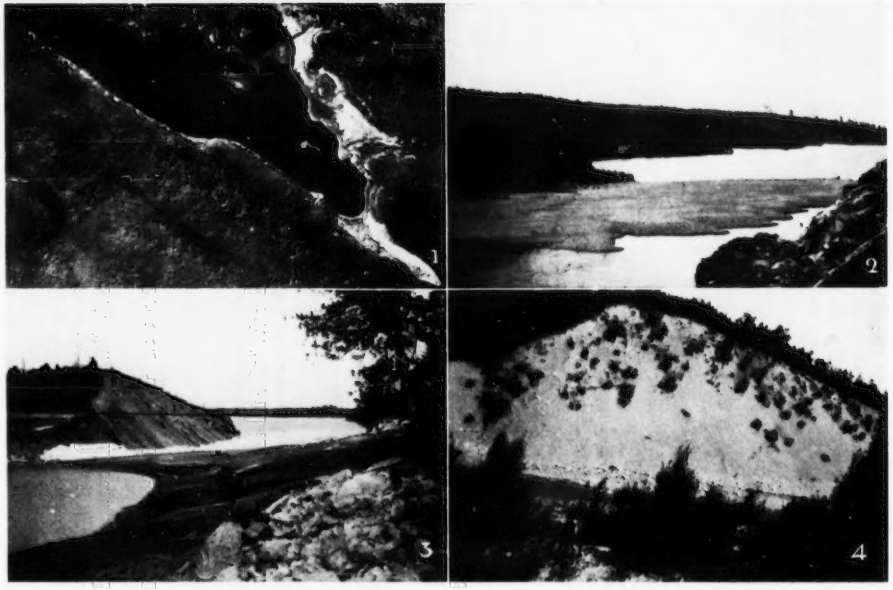

Fig. 1. Aerial photograph of Bass Lake. The old shore line can be traced by differences in the vegetation. The alluvial fan and delta extending into Low Lake are shown on the lower right. (Courtesy U. S. Forest Service No. 2207). Fig. 2. Alluvial fan and delta in the foreground, Low Lake in distance. May, 1925. (Courtesy Cyko). Fig. 3. The gully formed by the draining of Bass Lake into Low Lake as viewed from the beach of the former. May, 1925. (Courtesy Cyko). Fig. 4. South facing slope of the gully between Bass Lake and Low Lake. August, 1934.

55 feet in 10 hours, exposing large areas of the glacio-lacustrine sediments along the old beaches and in the bays of the former lake. A ripple-surfaced cobble, gravel and sand delta was formed in the west end of Low Lake, and a gorge about 250 feet wide was formed between the lakes.

The partial drainage of Bass Lake made available the following new habitats for plant invasion: 1. The gully that was cut through the moraine separating Bass and Low Lakes. The soil of the north slope is coarse gravel and cobbles with some boulders up to 2 feet in diameter. The south slope is largely outcropping rock. 2. The alluvial fan which merges into a delta in Low Lake. The soil ranges from cobbles near the moraine to fine sand near the edge of the delta. Many of the giant asymmetrical current ripples that transverse this fan measure 50 to 60 feet from crest to crest. These have long lee slopes on which the soil grades from cobbles and coarse gravel in the troughs to gravel and sand near the crests, and stoss slopes of fine gravel and sand. 3. The bare rock that formerly made up much of the steep lake shore. This rock is largely Algomian granites and syenites and Ely greenstone. 4. The talus slope that lies at the base of the cliffs that edge part of the lake. This talus is made up of large angular Archean rock fragments. 5. The level and the slightly sloping sedimentary beds of silt and sand in the two drained north arms and along the north shore of the present lake. Several deep gullies have been eroded in these deposits; in these the laminated nature of the beds can be clearly seen. Cross bedding is also evident in many places. At various levels in these deposits are seams of peat varying in thickness from a few inches to 6 feet. Some of these peat strata seem to be of open swamp origin while others are made up largely of jack pine forest litter. 6. The old cobble and boulder beaches of the lake at its former level. 7. A small boulder covered island that was exposed by the lowering of the lake level. 8. The narrow drained west arm of the lake. The soil here is predominantly gravel.

Plant Invasion on the Newly Formed Habitats

In the draining of Bass Lake the unconsolidated soil material underwent three major changes: (1) The material was resorted and several types of skeletal soils ranging from boulders to clays deposited. (2) The skeletal soils, because of the difference in origin of the component materials, vary from unmodified parent boulder clay to somewhat weathered soil material. (3) The skeletal soils and especially the unaltered bottom soils in many instances changed from a hydromorphic to orthomorphic, xeromorphic or intermediate condition. These changes render the tracing and evaluation of the various edaphic and pedologic factors extremely difficult.

With the limited means available for this study it was therefore deemed impractical to definitely relate the soil factors to the types of plant succession. Historically, the raw glacial soil of the sides of the gully and the surface of the delta form a habitat on which succession is certainly primary. The other habitats have accumulated varying quantities of organic matter and weathered soil material from erosion and drainage of the surrounding region and the light

plankton growth that occurs in the soft waters of a lake of this type. Succession upon these habitats is doubtfully secondary in nature.

1. *The gully.* In 1934 the woody vegetation of the gully floor consisted of *Populus tremuloides, P. balsamifera, Betula papyrifera, Alnus incana,* and several species of willows. The most abundant ground cover species were horsetails, *Equisetum hyemale* var. *affine* and *E. arvense.* Species of secondary importance were *Anaphalis margaritacea, Gnaphalium polycephalum, Aster multiflorus, Solidago serotina, Trifolium hybridum,* and *Agrostis hiemalis.* On the brushy south edge of the gully floor were numerous seedlings of jack, Norway and white pine and of balsam fir. On the coarse morainic soil of the north slope of the gully the commoneest woody species recorded in 1934 was *Salix longifolia.* Other species present were *Populus tremuloides, P. grandidentata, Betula papyrifera, Prunus virginiana, P. pennsylvanica, Rhus Toxicodendron, Diervilla Lonicera, Lonicera canadensis, Acer spicatum,* and *Cornus rugosa.* On the dry face of the slope the commonest herbaceous species were *Equisetum hyemale* var. *affine, Chenopodium album, Polygonum cilinode.* On the moister bottom portion of the slope were *Gnaphalium uliginosum, Anaphalis margaritacea, Epilobium angustifolium, Carex vulpinoidea,* and *Scutellaria lateriflora* (Fig. 4). The south slope of the gully is largely bare rock capped with laminated sand and silt. The only invaders here were a few white birches. Little vegetational change was noted in 1936 and 1939.

2. *The alluvial fan and delta.* By 1934 the coarse gravelly and cobbly soil of the central portion supported only a sparse vegetation, confined mostly to the lee slopes of the giant ripples and their troughs (Fig. 6). The characteristic woody species were *Salix Bebbiana, S. discolor, S. lucida, S. balsamifera,* and *Alnus incana.* In the deeper and moister troughs were occasional colonies of *Typha latifolia, Scirpus atrocinctus,* and *Carex Bebbii.* In the drier troughs were *Agrostis hiemalis, Poa palustris,* and *Juncus tenuis.* On the lee slope were occasional seedlings of the forest trees, *Betula papyrifera, Populus tremuloides,* and *P. balsamifera.* With these was a scattering of herbs including *Polygonum cilinode, Oenothera biennis, Epilobium angustifolium, Potentilla monspeliensis,* and *Aster macrophyllus.* In 1934 only one conifer seedling, a white spruce, was found, but by 1939 a considerable number of white cedar, balsam fir and white pine seedlings had appeared. Other species that have invaded this area since 1934 are *Sambucus racemosa, Amelanchier humilis, A. laevis,* and several herbs already noted for the gully. On the finer soils at the edge of the delta the following wet soil species had established themselves by 1934: *Thuja occidentalis, Myrica Gale, Spirea alba, Scutellaria lateriflora, Mentha canadensis, Epilobium palustre, Muhlenbergia racemosa, Impatiens biflora, Bidens cernua* and *Carex retrorsa.* Present also were such ubiquitous species as *Epilobium angustifolium, Panicum capillare, Sonchus arvensis, Rumex crispus, Polygonum aviculare, Sisymbrium altissimum, Echinochloa crusgalli, Poa compressa, Rubus strigosus,* and *Ranunculus pennsylvanicus.* On the drier sandy soils the most abundant species was *Oenothera biennis,* and next in importance, *Agrostis hiemalis* (Fig. 5). These species were abundant on the lee slopes of the ripples and occasionally appeared in the troughs. During the period from 1934 to

1939, there was a marked reduction in the number of *Oenothera* plants on the permanent quadrats.

3. *The bare Archean rocks of the old lake basin.* The only plants found upon this habitat were a few aspens and white birches that had established themselves in the cracks and crevices.

4. and 6. *The talus slope and the old cobble and boulder beaches.* By 1934 these habitats had been taken over almost exclusively by white birch. The only other trees present were occasional aspens, balsam poplars, and pin cherries. At that time the stand was 6 to 8 feet high, and the individual trees averaged about one inch in diameter. By 1939 the stand had grown to a height of 12 feet and was considerably thinner. The individual birches averaged about 2 inches in diameter, while some of the aspen and balsam poplar had diameters at breast height of 4 to 5 inches. In this stand were 3- and 4-year old white spruce and balsam fir. The undergrowth of the old cobble beaches was sparse, consisting of scattered plants of *Vaccinium pennsylvanicum, Galium labradoricum, Anaphalis margaritacea, Agrostis alba, A. hiemalis, Fragaria virginiana, Poa palustris, Onoclea sensibilis,* and *Muhlenbergia racemosa.* The lower talus slopes have in addition to these many of the moist forest herbs (Fig. 7).

5. *The laminated sand and silt deposits.* The flat or slightly sloping surface of these beds consist chiefly of two soil classes, fine sandy silt, and a coarse sand with a little gravel. By 1934 the areas of the finer sediments had been covered with a fairly dense stand of sedges and grasses. The most abundant species were *Poa palustris, P. compressa,* and *Agrostis hiemalis.* Of lesser importance were *Hordeum jubatum, Poa pratensis, Panicum Lindheimeri, Agropyron repens, Calamogrostis canadensis, Carex filiformis, C. Bebbii, C. adusta,* and *Scirpus atrocinctus.* Present also was a scattered population of forbs *Anaphalis margaritacea, Oenothera biennis, Gnaphalium uliginosum,* and *Polygonum lapathifolium* (Fig. 9). Small areas of this sandy soil were dominated by mosses, *Polytrichum juniperinum, P. alpinum,* and *Ceratodon purpureus.* By 1939 the herbaceous flora had changed little, but seedlings of the following common forest trees had appeared: *Betula papyrifera, Pinus Strobus, P. resinosa, P. Banksiana, Picea canadensis, Populus tremuloides,* and *P. balsamifera.*

The ground cover of the coarser soils in 1934 was largely *Equisetum arvense* with scattered plants of *Anaphalis margaritacea, Gnaphalium uliginosum, Phragmites maximum, Solidago serotina,* and *Juncus balticus* var. *littoralis.* The willows, *Salix lucida, S. Bebbiana,* and *S. balsamifera* were fairly common. Present also were the aspen, the balsam poplar and a few seedlings of jack pine (Fig. 8). By 1939, the balsam fir and other tree species that have been previously mentioned as invading the finer soils had established themselves. The sides of the numerous gullies that had been cut through these sediment were in 1934 sparingly colonized with the herbaceous species of the sand plain and birch, aspen, balsam poplar, and willows. By 1939, all but the steepest slopes were densely covered with vegetation.

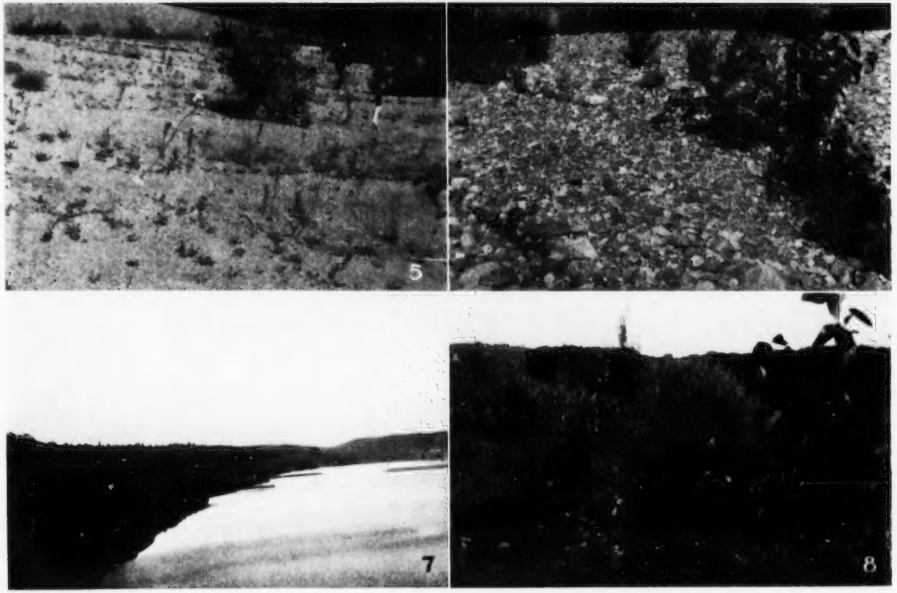

Fig. 5. Quadrat on coarse to medium sand showing the abundance of *Oenothera biennis*. August, 1934. Fig. 6. Coarse gravel and cobble area of the alluvial fan showing vegetation in the troughs of the giant ripples. August, 1934. Fig. 7. South shore of Bass Lake in August, 1936, showing birch-aspen stand on exposed talus and gravel. Fig. 8. Area of coarse sand on sedimentary plain along the north side of Bass Lake showing the abundance of *Equisetum arvense*. August, 1934.

7. *The island.* The soil of the recently exposed island in Bass Lake in quite similar to that of the sedimentary plain just described except that the sediments contain a considerable number of boulders and cobbles. The zonation on this island is well marked, showing the effect of the water level upon the survival of some of the common invading species. At the beach line is a zone composed mostly of *Typa latifolia* with a few plants of *Glyceria borealis* and *Equisetum limosum.* Directly inside this is a second zone in which the predominant plant is *Scirpus atrocinctus.* A third zone, slightly higher above the water level, is populated by the shrubs *Alnus incana, A. crispa, Salix lucida,* and *S. Bebbiana* together with a few balsam poplars. The central and highest zone is a thicket of aspen and birch with *Equisetum arvense* as the principal ground cover species (Fig. 10).

8. *The drained west arm.* The gravelly soil of the central and lower portion of the narrow drained west arm is covered with a dense stand of willows and tag alder. On the higher and outer portion, which merges into the talus slope already described, is a nearly pure stand of white birch.

Sunken Lake

Location, Physiography, and Recent History

Sunken Lake, formerly known as Bachelor Lake, is located in west-central Itasca County (Sec. 16, T147N, R27W) about a mile and a half north-northwest of Cut Foot Sioux Lake and not far from the northwest shore of Lake Winnibigoshish. Sunken Lake has an elevation of slightly more than 1300 feet and drains indirectly into the Mississippi River through the two previously mentioned lakes. The immediate region is characterized by recessional moraines of the young gray (Fifth Wisconsin) drift (Leverett and Sardeson 1917, 1932). A narrow gravel moraine of this drift forms the eastern shore of Sunken Lake. Prior to 1914, the lake drained over this moraine, and the water level was held considerably higher than that of the adjacent lakes.

Extensive logging operations were carried on in the vicinity of Lake Winnibigoshish in 1914 and 1915. At this time the commercially important timber was removed from around Sunken Lake by the Northland Pine Company of Minneapolis. A road for hauling the logs to the mill on Big Cut Foot Sioux Lake was built over the narrow moraine that forms the east shore of the lake. To lessen the grade, a cut was made through the crest of this moraine. About May 20th, in the spring of 1915, water from the heavy rains so raised the water level of the lake that drainage began through this newly constructed road cut. Erosion of the loose morainic gravel became so rapid that within a few hours this stream washed out a V-shaped section of the moraine lowering the water level of the lake 33 feet. It is probable that the adjoining muskegs drained more slowly and that a stream of considerable size flowed through the newly formed gully for several weeks (Fig. 17).

The catastrophic partial drainage of Sunken Lake created several new physiographic features and altered many that had been associated with the

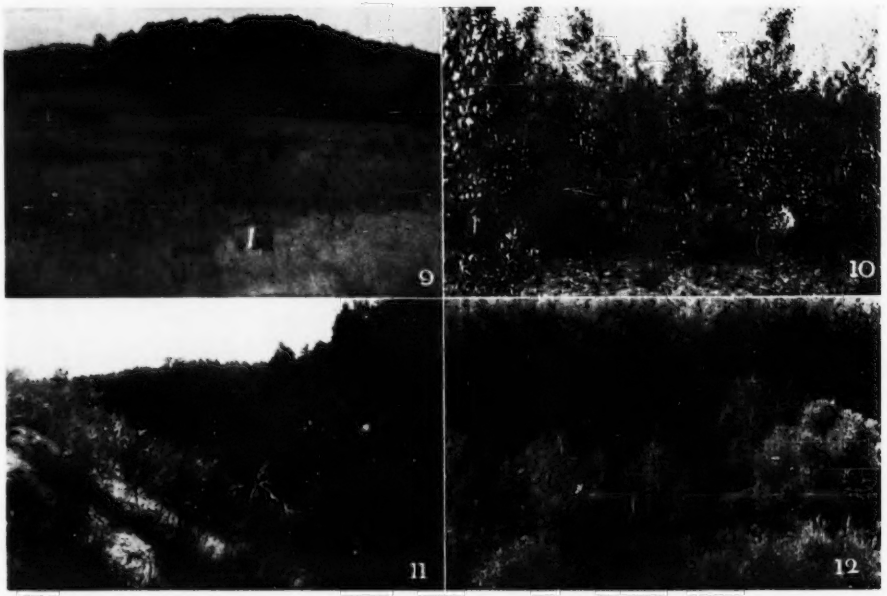

Fig. 9. Area of fine sandy soil on sedimentary plain along north shore of Bass Lake showing abundance of grasses and sedges. August, 1934. Fig. 10. Birch-aspen thicket on the higher portion of the recently exposed island in Bass Lake. Similar associations occur on the newly exposed beaches. August, 1936. Fig. 11. South facing slope of gully in August, 1934. Principal species: *Equisetum hyemale* var.*affine*, *Salix longifolia*, and *Oenothera biennis*. Fig. 12. North facing slope and trough of gully in August, 1934. Principal woody species: white pine, aspen, birch, and alder.

lake at its former level. The most important of these changes are as follows: 1. A V-shaped gully or gorge was cut through the impounding moraine. This gully is 39 feet deep, about 120 feet across at the crest of the moraine, and about an eighth of a mile long. 2. Immediately below the gully an alluvial fan was deposited, having a radius of about one-eighth mile and a maximum depth of 8 feet near its point of origin. A portion of the fan buried a mature cedar and spruce bog. 3. An area of old lake bottom was exposed between the former and present beaches of the main lake. This strip of exposed lake bottom varies in width from 50 to 300 feet. 4. The partly floating fringing sedge and heath mats of parts of the old lake shore were left several feet above the present lake level. These are now quite dry and rest directly on inorganic soil. 5. The shallow south arm of the old lake which was nearly covered with floating heath and sedge mats drained slowly by seepage through the narrow gravel bar that separated it from the main lake and left these mats of vegetation drained and stranded on the bottom. 6. The entire west arm of the lake was drained, leaving only a few ponds in the depressions.

As a result of these physiographic modifications several different kinds of habitats were formed from unmodified glacial till: the sandy alluvial fan; the dry gravelly sides of the gully; the moist sandy bottom of the gully. Successions initiated on such habitats are considered primary. Three other types of newly formed habitats show in their soil the effect of former plant growth: the drained heath-sphagnum bogs that surrounded the south and part of the west arm of the old lake; the center of the south arm of the old lake; and the exposed lake bottom between the old and new beaches on the existing lake and the entire bottom of the drained west arm. The soils of these habitats are, respectively: unconsolidated peat with much dry sphagnum; muck, devoid of organic structure; and sand, silt and clay with some organic increment from plankton and aquatic plants. Successions beginning on these last three soil types are considered secondary.

Invasion and Succession on the New Habitats

1. *The gully.* Nineteen years after the formation of the gully (1934) its bottom was a dense thicket of willows and tag alder, *Alnus incana*, with many balsam poplars and some white birch. These woody species densely shaded the whole gully floor. On the moist soil along the narrow stream (about 3 feet wide) that runs through the gully were occasional plants of two members of the open marsh and shore flora, *Carex vesicaria* and *Typha latifolia*. More abundant were the bog forest herbs, *Lycopus americanus*, *Pilea pumila*, *Epilobium palustre*, and *Equisetum arvense*. Mosses and liverworts covered the stream margin. Away from the stream and covering all the drier gravelly soil of the gully bottom was a thick carpet of the scouring rush, *Equisetum hyemale* var. *affine*. The upland flora was represented by occasional plants of *Aster macrophyllus*, *Chenopodium leptophyllum*, *Pyrola rotundifolia* var. *americana*, and *Rubus strigosus*. The drier gravelly south-facing slope of the gully was also dominated by *Equisetum hyemale* var. *affine*, but here the sandbar willow,

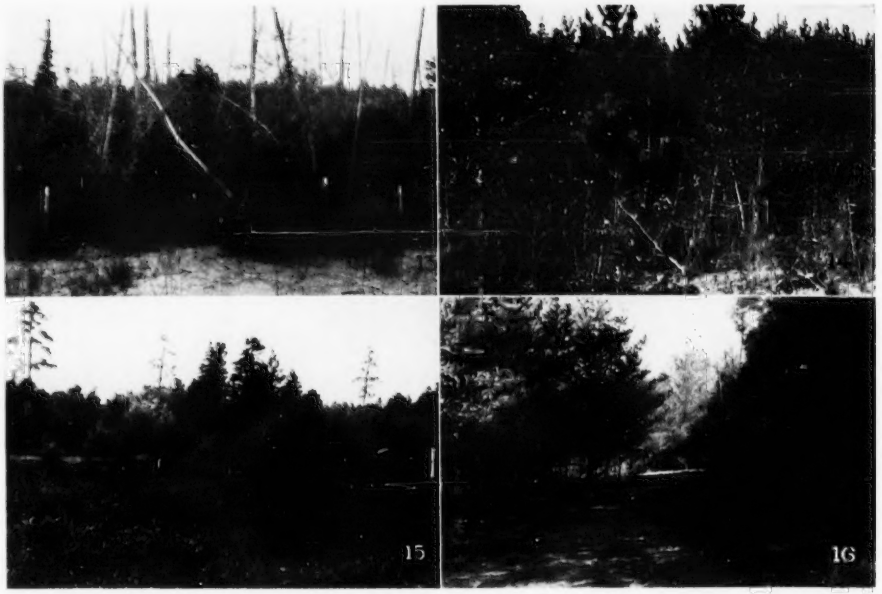

Fig. 13. Quadrat adjajcent to the buried cedar-spruce bog showing abundance of *Equisetum hyemale* var. *affine*. Fig. 14. Vegetation on exposed sandy lake bottom. Common species: aspen, balsam poplar, Norway pine, white pine, and jack pine. August, 1936. Fig. 15. Quadrat in the drained sphagnum-heath bog. Note the invading pines and the absence of deciduous forest species. August, 1936. Fig. 16. Exposed sandy lake bottom along northwest shore of Sunken Lake. Former beach in center, old forest on right, newly established jack pine stand on left. September, 1939.

Salix longifolia, was also an important species (Fig. 11). Many of the herbs that are common in openings of pine forests were also present, *Fragaria virginiana, Rubus strigosus, Apocynum androsaemifolium, Chenopodium leptophyllum, Oenothera biennis,* and *Epilobium angustifolium.* The only grass noted was *Muhlenbergia racemosa.* The vegetation of the north-facing slope was similar but denser; here a few Norway pine were found (Fig. 12).

By September, 1939, conditions on the floor of the upper half of the gully had drastically changed. Beaver had constructed three dams across the stream, the lower two of these impounding heads of 18- and 24-inches of water. These

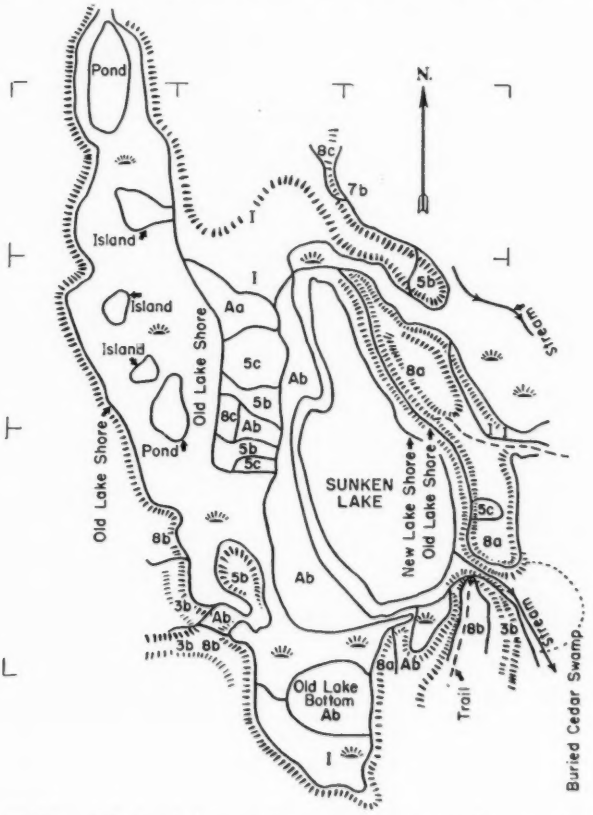

Fig. 17. Map of Sunken Lake area. Key to vegetation types: A—aspen, 1—brush, 3—birch, 5—jack pine, 7—spruce, 8—Norway pine, 9—white pine, a—reproduction, b—saplings, c—poles. (Courtesy U. S. Forest Service).

flooded a considerable area with the consequent destruction of the herbaceous ground cover. None of the woody species, however, had as yet been cut by the beaver. The balsam poplar, Bebb's Willow, tag alder, and white birch had grown to a height of 20 feet and some of the balsam poplars had attained a diameter of 5 inches. The herbaceous flora of the non-flooded part of the gully had changed little except for the addition of occasional plants of *Aster junceus*, *A. multiflorus*, and *Galium boreale*. On the slopes of the gully numerous small jack pine, balsam poplar, and birch had appeared. A small Norway pine, noted in 1934, was now 6 feet high. *Agrostis alba* and *Prunus pumila* were noted for the first time.

2. *The alluvial fan*. The larger part of the alluvial fan was composed of coarse sand and showed no trace of previous vegetation. At its eastern edge, however, was a tangle of dead and down white cedar and spruce trees, the remains of the buried bog. The giant ripple marks which originally gave a slightly undulating surface to the alluvial fan are now almost obliterated. In 1934 a check of the vegetation on this nearly flat sandy surface showed that as on the sides of the gully, the dominant ground cover species were the horsetails (Fig. 13). On the fan, however, *Equisetum arvense* and *E. hyemale* var. *affine* were about equally abundant. Scattered throughout the *Equisetum* mat were the typical open pine forest species, *Carex pennsylvanica*, *Oenothera biennis*, *Agrostis hyemalis*, *Fragaria virginiana*, *Poa palustris*, *Pteridium latiusculum*, *Cynoglossum boreale*, *Solidago* sp., *Aster macrophyllus A. Lindleyanus*, *Anaphalis margaritacea*, *Bromus ciliatus*, *Pyrola secunda*, and *Pyrola rotundifolia* var. *americana*. Likewise, the woody species that had established themselves were common trees and shrubs of the coniferous forest, *Pinus resinosa*, *Betula papyrifera*, *Populus tremuloides*, *P. balsamifera*, *Prunus pennsylvanica*, *P. virginiana*, *P. pumila*, *Rosa blanda*, and *Rhus toxicodendron*.

In 1939 the most noticeable change was the marked growth of the Norway pine on quadrat 3. Beneath this tree, now 7 feet tall, a good turf of *Carex pennsylvanica*, a typical pine forest sedge, had formed. First noted on the alluvial fan at this time were *Amelanchier humilis*, *Senecio balsamitae*, *Salix Bebbiana* and *Polygonum* sp.

3. *The drained sphagnum heath mats*. Although these mats are now quite dry, the original heath components are still flourishing. *Chamaedaphne calyculata* is the predominant species with *Andromeda glaucophylla* and *Ledum groenlandicum* of lesser importance. Most of the sphagnum is now dead and the old hummocks are covered with lichens of the genus *Cladonia*. From increment borings it is evident that some tamarack and a few pines had established themselves on the shoreward edge of these mats before the drainage of the lake. In 1934 one of the tamaracks showed 74 growth rings. The growth rate of these older trees, as evidenced by the width of the annual rings, was greatly accelerated upon the drainage of the heath mats. A few very narrow rings were laid down between 1910 and 1916; these mark the years of heavy infestation of the larch sawfly. Although almost no herbaceous vegetation has estab-

lished itself on the loose, highly organic soil of the heath mats, a scattered stand of white, jack, and Norway pines, white spruce and a few tamaracks has appeared. Jack pine is the most abundant species. Good growth has been made on this loose organic soil; by 1939 many of the pines had reached a height of 15 to 18 feet (Fig. 15).

4. *The center of the drained south arm.* That portion of the drained south arm of the lake that lies inside the fringing drained heath mats has a soil of sedimentary peat. This deposit of peat is about 9 inches thick and rests directly upon inorganic sediments. It was probably deposited by the aquatic plants and sedge mats that existed prior to the drainage of the lake. The substrates and the vegetation of this inner area can be divided into two types: the firm, drained peat directly inside the heath mat zone; the wet springy peat of the central portion. The outer drier zone is covered with a dense stand of *Populus tremuloides* in which are many clumps of *Salix discolor.* In 1934 these trees were found to be mostly 14 and 15 years old. Scattered throughout this stand were seedlings of *Picea canadensis* and *Quercus borealis.* The herbaceous and shrubby flora includes the shrubs *Spirea alba* and *Rubus strigosus* and the herbs *Eupatorium perfoliatum, Solidago serotina, Muhlenbergia racemosa, Carex tenella, Agrostis hyemalis, Epilobium angustifolium, Potentilla monspeliensis, Fragaria virginiana,* and *Scirpus atrocinctus.*

In the wet central part of the drained arm, aspen, with the exception of a few saplings, is lacking, its place being taken by the willows *Salix longifolia, S Bebbiana, S. balsamifera, S. candida, S. petiolaris,* and the tag alder, *Alnus incana.* There are a few scattered bushes of *Betula pumila* var. *glandulifera, Spirea alba,* and *Rubus strigosus.* The most common herbaceous species are *Solidago serotina, S. graminifolia, Aster salicifolius, A. junceus, Senecio aureus, Eupatorium perfoliatum, Dryopteris Thelypteris, Fragaria virginiana, Potentilla monspeliensis, Scirpus atrocinctus,* and *Carex filiformis.* The future trend of this area may be surmised from the occurrence of numerous seedlings and young trees of birch and jack pine on the drier spots.

5. *The exposed non-peaty lake bottom.* By 1934 the sandy lake bottom exposed between the old and new beaches of the present lake was densely colonized with balsam poplar. With this species were occasional birches, aspen, pin cherry, and jack, white and Norway pines. Herbaceous and shrubby species were present but not abundant. The most common shrubs were *Rhus glabra, Arctostaphylos Uva-ursi, Prunus pumila,* and *Rhus toxicodendron;* while the herbaceous flora was represented by *Antennaria canadensis, Anaphalis margaritacea, Potentilla monspeliensis, Solidago hispida,* and *Fragaria virginiana.* The only notable difference in the area in 1939 was the increasing predominance of the pines (Figs. 14 and 16).

At and near the present beach line, this newly exposed lake bottom has been taken over by the willows *Salix Bebbiana, S. longifolia, S. lucida, S. amygdaloides,* and the dogwoods *Cornus stolonifera* and *C. rugosa.* With these woody species are such hydrophytic herbs as *Typha latifolia, Cicuta bulbifera, Iris versicolor* and *Parnassia multiseta.*

The mineral soils in the bottom of the drained west arm support a flora very similar to that just described. Balsam poplar and aspen are the most conspicuous species. The shallower depressions in the basin have local communities of bog birch, willow and *Andromeda*. A few of the deeper depressions are still shallow ponds.

Summary and Conclusions

As a result of the catastrophic partial drainage of two northern Minnesota lakes, Bass Lake in St. Louis County, and Sunken Lake in Itasca County, areas of soil have been exposed upon which it is possible to study directly the invasion and succession of the northern coniferous forest species. In each case the drainage was accidentally accomplished during the logging operations by the washing out of a section of a moraine that had maintained the former lake level. Both nearly raw glacial soils and modified soils of various types were exposed. Because both of these lakes are surrounded by mature coniferous forest and the disseminules of the associated species are adequately available, it is possible to study the effect of the different soil types upon the invasion and establishment of the individual species. On the newly exposed glacial soils it is also possible to study the effect of early vegetational stages upon the establishment of the conifers. The results of field work carrier in in the Bass and Sunken Lake areas in the summers of 1934, 1936, and 1939 are summarized in the following paragraphs.

1. In the Bass and Sunken Lake areas there is little evidence of a general and orderly process of plant invasion and succession on nearly raw and slightly modified glacial soils. The nearest approach to a general pioneer stage on these soils is the extensive growth of the horsetails, *Equisetum hyemale* var. *affine* and *E. arvense*. Most of the woody deciduous species and many of the herbaceous species are able to invade these soils directly. The success of any individual species seems to depend upon the texture of the soil and the amount of available water.

2. The coniferous species follow the deciduous and herbaceous species closely on all the glacial soils. In several instances coniferous trees were noted that must have established themselves on these glacial soils almost immediately after their exposure. The effect of pioneer stages in preparing the soil for the coniferous species has been slight and appears to be mainly one of binding the soil and providing some shade for the coniferous seedlings. It is suggested that in the early stages of natural reforestation of such areas as Bass and Sunken Lakes, the apparent dominance of non-coniferous species may be due to the ability of these species to invade an area rapidly principally because of the structure of their disseminules and not because slightly modified glacial soils are more suited to these species than they are to the conifers.

3. On the organic soils of the Sunken Lake area, forest invasion has been of three types. On the loose peat of a drained sphagnum-heath bog the pines, white spruce, and tamarack have successfully established themselves; alder,

poplars, willows, and the herbaceous flora have not; drained sedimentary peat has been taken over largely by aspen; wet sedimentary peat, by willows and alder.

4. Old talus slopes, dry cobble beaches, and well drained areas of coarse gravel have been invaded by white birch to the exclusion of almost all other woody species.

5. Balsam poplar is the most successful invader on the well drained inorganic sediments of the old lake bottoms. In places jack pine and aspen are also abundant. Wet inorganic sediments are usually colonized by willows.

ACKNOWLEDGMENTS

The writers wish to acknowledge the research grant made in 1936 by the Minnesota Academy of Science, which has aided materially in making this study possible. The writers also wish to acknowledge the aid, suggestions, and criticisms extended by Dr. W. S. Cooper, Dr. Hardy W. Shirley, Dr. G. A. Thiel, Mr. George Farley, Mr. Frank Koschak, The Minnesota Historical Society, The U. S. Forest Service, and the Cyko Art Studio.

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Peloric Flowers in Cypripedium reginae Walt.

J. T. Curtis

The occurrence of teratological flowers in *Cypripedium* and related genera has been noted by many observers. The unusual forms are of interest since they shed much light upon the basic or primitive structure of this section of the family *Orchidaceae* and are of great value in phylogenetic studies. Masters (1887) studied and described a large number of teratological specimens of various orchids. He recognized four types of malformation and classified them under the following heads: oligomery (reduction of parts), pleiomery (increased number of parts), displacement (change in position of parts), and peloria (tendency towards regularity of form). Peloria may be achieved by a reversion of irregular parts to the regular form, or by an increase in number of the irregular parts. Thus, in a generalized orchid flower, with two petals of ordinary shape and the other modified into a lip, regularity could be reached by three lip-like petals and none of usual form or by no lip and three ordinary petals. The last type is perhaps the most interesting, since the reversion from an irregular to a regular flower by simplification is commonly thought to indicate a throwback to the primitive condition.

As far is is known, only one case of regular peloria in the genus *Cypripedium* has been recorded. Asa Gray (1866) described a flower of *Cypripedium candidum* Muhl. which was regular, symmetrical and complete, but dimerous. The closest approach to a perfectly regular, trimerous *Cypripedium* flower was one of *Cypripedium reginae* Walt. reported by Bastin (1881) which had three equal sepals, three nearly equal petals, three anthers, but only two staminodia.

In July, 1939, a perfectly regular flower of *Cypripedium reginae* was discovered in a tamarack-spruce bog in the Gillen Refuge in northern Michigan. The flower was borne by one stem from a rhizome bearing two other flowering stems, both of which had normal flowers. Many other individuals of the species were in bloom in the bog at the same time, but no other teratological flowers could be found.

Three distinct, equal sepals were present, as compared to the two of a normal flower. Alternating with the sepals and inserted above them were three regular, equal petals. The petals and sepals were of the same length, but differed in width and shape, as can be seen in Fig. 1. Both were pure white, with no trace of the rose-purple blotch characteristic of the inflated lip of normal flowers. Three sterile stamens, or staminodia, occupied the next whorl of flower parts. These staminodia were all alike, and were arranged opposite to the sepals and alternate with the petals. They resembled the normal type in coloring, but differed in being oblong rather than cordate.

Alternating with the staminodia were three fertile stamens, with their terminal portions and anther cases free, but with the basal parts in close union with the pistil. Of all the flower parts, the pistil showed the greatest modifications. It was a perfectly regular structure occupying the center of the flower. The equally three-lobed stigmatic surface was at the inflated outer end of a trumpet-shaped style; the lobes of the stigma were opposite to the staminodia. The ovary did not differ in outward appearance from that of a normal blossom.

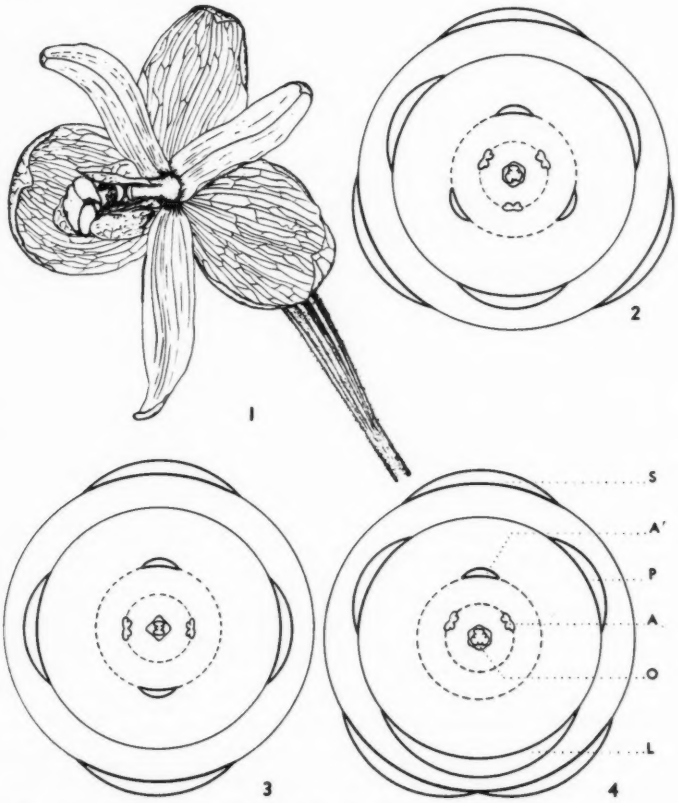

Fig. 1. Trimerous, peloric flower of *Cypripedium reginae* Walt.

Figs. 2-4. Floral diagrams of peloric and normal flowers of *Cypripedium reginae* Walt. 2. Trimerous peloric flower of 1939. 3. Dimerous peloric flower of 1940. 4. Normal flower. S = sepal, A′ = sterile anther, P = petal, A = fertile anther, O = ovary, L = lip.

All flower parts except the staminodia and the ovary were pure white, with a peculiar opaque, milky appearance to the fleshy portions of stamens and pistil. The staminodia had the usual yellow ground color and light brown spotting that is found in typical flowers.

A floral diagram of the peloric flower just described is shown in Fig. 2. It can be seen that this diagram is identical with the theoretical basal plan of all orchids as postulated by Darwin (1877) and Gerard (1878), who believed that the ancestral form of the orchid had three sepals, three petals, six stamens in two whorls and three carpels with three stigmas. A normal flower is diagrammed in Fig. 4. The two lower sepals are fused into one, the petal normally alternate with the two fused sepals is greatly modified into the inflated lip, two of the stamens of the outer whorl are lacking, and the stamen of the inner whorl on the same side is also missing.

Some investigators believe that in the usual *Cypripedium* flower the two missing staminodia are fused with one of the petals to form the lip. No vascular dissections were made on the present flower and hence no conclusions regarding this problem could be drawn.

The plant bearing this flower was carefully marked so that its future behavior could be observed. In the related tropical genera *Paphiopedilum* and *Phragmopedilum*, teratological flowers usually appear at random and may never reappear upon the same plant. In a few cases (particularly in the Lindleyan genus *Uropedium*) the same plants may bear abnormal flowers annually. When the phenomenon is restricted to an isolated flower but it is probably due to some injury during bud formation or to unusual physiological disturbances at that time. When, however, the unusual forms recur annually, the character must be carried genetically by the vegetative parts, since new flower buds are produced upon separate stems arising from the rhizome tip.

It was therefore of great interest to find that the plant again produced a peloric flower in the 1940 season. Surprisingly enough, the 1940 flower, while perfectly regular, was dimerous, instead of trimerous as was the case in 1939. The flower parts corresponded exactly to those of the previous year in size and shape, including the oblong staminodia and trumpet-shaped style. A floral diagram of the 1940 flower is shown in Fig. 3. Whatever the genetical changes which brought about the reversion of the 1939 flower to the basic, primitive condition, there must have been still further changes causing the loss of one each of the flower parts in the 1940 flower.

The specimens are preserved in formalin-acetic acid-alcohol solution and are deposited in the herbarium of the University of Wisconsin. The author wishes to express his deep appreaciation to Mr. Martin J. Gillen of the Gillen Refuge, Michigan, for information regarding the above colony of *Cypripedium reginae* and for his aid in making its study possible, and to Dr. R. I. Evans of the Department of Botany, University of Wisconsin, for the drawing of the flower.

Summary

1. A peloric flower of *Cypripedium reginae* Walt. was found in 1939 in northern Michigan.

2. This flower was trimerous and was perfectly regular in all parts.

3. In 1940, the same plant exhibited another peloric flower which was dimerous, rather than trimerous.

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Notes on the Ecology and Geographical Distribution of Mississippi Myxomycetes

G. T. Johnson[1] and H. N. Andrews[2]

These notes are based upon approximately five hundred collections of slime molds made by the writers while they were collecting in Mississippi during June, 1939. The expedition on which these plants were obtained was not formed primarily to study this group, but the extreme abundance of fruiting specimens caused us to devote considerable time to their collection and general ecological relationships.

Smart (1937) reported that some of the material used in his study of spore germination in Myxomycetes came from Mississippi, and Macbride and Martin (1934) in addition to citing "Mississippi Valley" as the geographical area occupied by a number of species, definitely cite the occurrence of *Physarum gyrosum* in the state. These are the only Myxomycete records for Mississippi of which the writers are aware. In this report on the results of our study, a considerable number of forms are added to the known flora of the state.

The expedition covered much of Mississippi since it traveled south from Memphis, Tennessee, down the western side of the state, spent some time along the Gulf coast, and returned to Memphis by going up the eastern side and across the north. The counties cited with the list of species collected will show the extent to which the different regions of the state were covered. The pine forests were usually devoid of slime molds. Neither the hardwood stands scattered through the Coastal Pine region[3] nor the area occupied by the southeastern counties extending up as far as Meridian proved quite as fruitful as the west and east central swamps, although many collections were made in the former regions. The northeastern Prairie Belt was fairly barren and our collections from that part of Mississippi are sparse. The most prolific collecting was possible in the east central region of the state. Both the humid shady woods and the occasionally flooded bottom lands yielded an almost unbelievable abundance of this group. In the often flooded bottom lands, where the recurrent covering with water, together with considerable shade, apparently prevented the permanent establishment of an herbaceous flora, slime molds were particularly prominent. Decaying logs and twigs usually had seven or eight species in close proximity and the fructifications of a single species would often extend over an area of a few square feet.

We have wondered whether the profusion of Myxomycetes encountered on

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3 Phytogeographic regions from Lowe (1921, p. 57).

this trip is a constant yearly feature or whether it was due to peculiar conditions of the particular season we visited the state. In 1939 the mean precipitation of April was slightly below and that of May and June just slightly above the average for the past fifty-two years. The average monthly temperatures for those three months show only very slight variations from the average for the same period. It would thus seem, that as far as moisture and temperature are concerned, the factors affecting the slime mold flora at the time of our visit to Mississippi were entirely normal and that the same abundant development of this group might be expected by other collectors.

A list of the species and varieties collected, with the citation of the counties of Mississippi in which collections of each have been made follows immediately below:

EXOSPOREAE

CERATIOMYXALES

Ceratiomyxaceae

Ceratiomyxa fruticulosa (Mühl.) Macbr.—Copiah, Franklin, George, Grenada, Harrison, Jasper, Lamar, Lowndes, Pearl River, Tallahatchie, and Tunica.

Ceratiomyxa fruticulosa var. *arbuscula* Berk. & Br.—Harrison and Yalobush.

Ceratiomyxa fruticulosa var. *porioides* Alb. & Schw.—Stone.

MYXOGASTRES

PHYSARALES

Physaraceae

Fuligo septica (L.) Weber—Yalobusha.

Fuligo septica var. *flava* Pers.—Copiah, Kemper, and Marion.

Fuligo septica var. *rufa* Pers.—Grenada.

Craterium cylindricum Massee—Yalobusha.

Physarum viride (Bull.) Pers.—Clarke, Copiah, Franklin, Harrison, Hinds, Holmes, Stone, Tallahatchie, and Yalobusha.

Physarum nucleatum Rex—Lauderdale and Stone.

Physarum nutans Pers.—Clarke, Franklin, Holmes, Jasper, Lauderdale, Tallahatchie, and Yalobusha.

Physarum globuliferum (Bull.) Pers.—Clarke, Copiah, Grenada, Holmes, Jasper, Jones, Lauderdale, Pike, Stone, Tallahatchie, and Yalobusha.

Physarum pulcherripes Peck—Adams, Franklin, Grenada, Harrison, Jones, Lamar, Tallahatchie, and Wilkinson.

Physarella oblonga (Berk. & Curt.) Morg.—Stone.

Didymiaceae

Didymium xanthopus (Ditmar) Fr.—Kemper, Lauderdale, Pike, Stone, and Wilkinson.

Didymium nigripes (Link) Fr.—Yalobusha.

Diderma rugosum (Rex) Macbr.—DeSoto.

STEMONITALES

Stemonitaceae

Diachea leucopodia (Bull.) Rost.—DeSoto, Grenada, Holmes, and Pearl River.

Comatrichia typhoides (Bull.) Rost.—Copiah, Franklin, Grenada, Harrison, Holmes, Lamar, Madison, Pearl River, Pike, Stone, and Tunica.

Stemonitis splendens Rost.—Adams, Copiah, DeSoto, Grenada, Harrison, Hinds, Holmes, Lamar, Lauderdale, Madison, Monroe, Stone, Tallahatchie, Tunica and Wilkinson.

Lamprodermaceae

Clastoderma Debaryanum Blytt—Copiah and Stone.

LICEALES

Cribrariaceae

Lindbladia effusa (Ehr.) Rost. var. *simplex* Rex—Copiah.

Cribraria languescens Rex—Copiah, Hinds, and Pike.

Cribraria dictydioides Cooke & Balf.—DeSoto, Forest, Franklin, Jackson, Kemper, Lamar, Marion, Noxubee, Pearl River, and Pike.

Dictydium cancellatum (Batsch) Macbr.—Grenada, Franklin, Harrison, Hinds, Jones, Pike, Stone, and Yalobusha.

Tubiferaceae

Tubifera ferruginosa (Batsch) Gmelin—Franklin.

Reticulariaceae

Reticularia lycoperdon Bull.—Clarke.

Lycogalaceae

Lycogala epidendrum (L.) Fr.—Copiah, Franklin, Harrison, Kemper, Lauderdale, Monroe, Noxubee, Tallahatchie, Tunica, and Yalobusha.

TRICHIALES

Perichaenaceae

Ophiotheca chrysosperma Currey—Clarke.

Perichaena corticalis (Batsch) Rost.—Grenada.

Arcyriaceae

Arcyria cinerea (Bull.) Pers.—Adams, Clarke, Copiah, DeSoto, Forest, Franklin, Grenada, Hinds, Holmes, Jasper, Lauderdale, Monroe, Noxubee, Tallahatchie, Tunica, and Yalobusha.

Arcyria denudata (L.) Wettstein—Clarke, Copiah, DeSoto, Fanklin, Grenada, Hinds, Holmes, Jones, Lauderdale, Marion, Pearl River, Pike, Stone, Tallahatchie, Tunica, and Yalobusha.

Arcyria digitata (Schw.) Rost.—Carroll, Copiah, Franklin, Jones, Kemper, Lamar, Lauderdale, Noxubee, Tallahatchie, Tunica, and Yalobusha.

Arcyria nutans (Bull.) Grev.—Lamar.

Trichiaceae

Trichia scabra Rost.—Hinds and Tallahatchie.

Trichia favoginea (Batsch) Pers.—Kemper.

Hemitrichia stipitata (Massee) Macbr.—Clarke, Copiah, DeSoto, Franklin, Grenada, Hinds, Holmes, Jones, Lamar, Lauderdale, Marion, Pearl River, Perry, Stone, Tallahatchie, Tunica, and Yalobusha.

Hemitrichia vesparium (Batsch) Macbr.—Clarke, Copiah, DeSoto, Franklin, Hinds, Holmes, Jasper, Lamar, Lowndes, Madison, Marion, Noxubee, Perry, Tallahatchie, and Yalobusha.

Those species which, according to the geographical distribution given by Macbride and Martin (1934), have not been found in the southern United States are of especial interest. Some, like *Clastoderma Debaryanum*, are undoubtedly often overlooked because of their very minute size. Others, like *Ophiotheca chrysosperma* and *Perichaena corticalis*, are not easily discovered, since they either occur on the inner side of the bark of trees or are inconspicuous because of protective coloration. Additional Myxomycetes which have not previously been collected from the Mississippi region are: *Cribraria languescens*, *Diderma rugosum*, *Physarum pulcherripes*, *Reticularia lycoperdon*, and *Trichia scabra*.

Some species, on the other hand, were found in abundance at almost every locality. The widespread distribution of these species throughout the state is indicated in the table (a more detailed study would probably eliminate most of the vacant squares). In some localities all the species collected were found, not only in abundance at the place visited, but also on a single log. Although great ecoogical conclusions are not justified from the examination of only five hundred collections, the constant association of so many species indicates that these form a definite society in the June display of Mississippi flora in normal years.

Species Collected	Collections Made at Locality Number																		
	24[4]	3	6	7	8	9	11	12	15	20	24	25	31	34	37	39	40	45	46
Arcyria cinerea	×[5]	×	×	×	×	×	×	×					×			×	×	×	
Arcyria denudata	×	×	×	×	×		×	×	×	×		×	×		×	×	×	×	×
Arcyria digitata		×	×		×			×	×					×	×		×	×	×
Ceratiomyxa fruticulosa		×	×	×				×	×		×			×					
Comatrichia typhoides		×		×	×	×		×		×	×	×		×					
Dictydium cancellatum							×		×	×	×	×	×		×			×	
Hemitrichia stipitata	×		×	×	×	×	×		×			×	×	×	×	×	×		×
Hemitrichia vesparium	×		×		×	×	×	×						×	×	×		×	×
Lycogala epidendrum		×	×					×	×		×		×	×			×		×
Physarum globuliferum			×	×				×		×	×	×	×		×	×	×		×
Physarum pulcherripes			×	×					×		×	×			×		×		
Physarum viride			×				×	×	×		×	×					×		×	×
Stemonitis splendens		×	×	×	×	×	×	×			×	×	×	×			×		×

4 Gaps occur in the serial list of localities because collections of other groups of plants were made in habitats where Myxomycetes did not grow.

5 The sign "×" indicates that collections of the species listed were made in the locality designated.

Summary

1. This paper contains a report on approximately five hundred collections of slime molds obtained in Mississippi in June, 1939. The specimens represent thirty-seven species and varieties in twenty-five genera, most of them being additions to the known flora of the state.

2. Mississippi stations for *Clastoderma Debaryanum, Cribraria languescens, Diderma rugosum, Ophiotheca chrysosperma, Perichaena corticalis, Physarum pulcherripes, Reticularia lycoperdon,* and *Trichia scabra* are several hundred miles from their previously known geographical ranges.

3. *Arcyria cinerea, A. denudata, A. digitata, Ceratiomyxa fruticulosa, Comatrichia typhoides, Dictydium cancellatum, Hemitrichia stipitata, H. vesparium, Lycogala epidendrum, Physarum globuliferum, P. pulcherripes, P. viride,* and *Stemonitis splendens* seem major elements of an ecological society to be associated with the June display of Myxomycetes in Mississippi.

ACKNOWLEDGEMENT

The writers wish to acknowledge their indebtedness to Dr. G. W. Martin, who personally studied a representative specimen of each species reported in this paper and either confirmed our own determination or redetermined the material.

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A Generic Review of the Family Apioceratidae with a Revision of the North American Species (Diptera - Brachycera)

Mont A. Cazier*

The flies belonging to the family Apioceratidae have been primarily of interest to the dipterologist because of their relative scarcity, their unusual characteristics, and their controversial position in dipterous phylogeny. Few families have undergone equally chaotic phylogenetic arrangements, over a period of about one hundred years, and still emerged in as unsatisfactory a condition as have the *Apioceratidae*. During the speculative course of these dissertations this family has been placed in, or approximate to, a number of other families; none of these arrangements, however, appears to be entirely in agreement with the facts as they are now understood.

The writer takes this opportunity to express his gratitude and indebtedness to Dr. T. H. G. Aitken, Mr. P. H. Timberlake, Mr. K. L. Maehler, Dr. M. T. James, Mr. C. D. Michener, Mr. F. H. Parker, Dr. R. H. Painter, Dr. E. C. Van Dyke, Mr. A. T. McClay, Mr. G. E. Bohart, Dr. R. M. Bohart, Dr. E. S. Ross and Mr. K. S. Hagen for the loan of specimens from their private collections, and to Mr. E. P. Van Duzee of the California Academy of Sciences, Dr. D. W. Pierce of the Los Angeles Museum of Arts and Science, Dr. R. H. Beamer of the University of Kansas, Mr. Nathan Banks of the Museum of Comparative Zoology, Dr. E. A. Chapin and Mr. C. T. Greene of the United States National Museum, and Mr. C. F. Harbison of the San Diego Museum of Natural History for the privilege granted him of studying types and other material in their charge. The writer would like also to express his thanks to Prof. E. O. Essig and Dr. E. G. Linsley for their aid and constructive criticisms so willingly given during the preparation of this manuscript, and to Dr. E. C. Van Dyke under whose supervision the work was originally begun. Thanks are also due Dr. R. Craig and Dr. T. G. Aitken for their kindness in photographing the species.

History

The first species was described by Wiedemann in 1830 and was placed in the asilid genus *Laphria* as *L. brevicornis*. Macquart (1838) perceived from Wiedemann's description that the species was not a species of *Laphria*, and, as he did in many other cases, erected a new genus, *Tapinocera* for *L. brevicornis* Wied. without actually studying a specimen. Consequently, when he eventually obtained specimens of his *Tapinocera* (=*Laphria brevicornis* Wied.) he failed to recognize them as such and redescribed them as *Pomacera* (1846) and erected the family Pomaceridae for them. However, Westwood (1835) had previously described the genus *Apiocera* for two new Australian species. Bigot (1857) regarded the group as of family rank, as had Macquart; he placed them in his "Asilides," discarding Macquart's *Pomacera* (1846) for *Apiocera* Westwood (1835) and established the family Apioceridae (Apios,

* This paper was written while the author was at the University of California, Berkeley, California.

a pear; cerata, horn). This name has been subsequently emended by Brues and Melander (1932) to the more correct grammatical form Apioceratidae. The type species of the genus *Apiocera* is *A. fuscicollis* Westwood [=*Apiocera brevicornis* (Wied.)], vide Hardy (1933) as designated by Coquillett (1910).

Philippi in 1865 described as new and figured the Chilean genus *Megascelus* as a mydaid.[1] Hermann (1909) recognized the genus as a member of the Apioceratidae and included it as such in his discussion of the family. After a consideration of the original description and the figures given it seems necessary to point out that certain features of this genus are common to both the Apioceratidae and Mydaidae. The ocelli are apparently absent ("vertex concave"), the terminalia small, and the shape subparallel and narrow as in certain genera of the Mydaidae *(Nemoneura* and *Nemomydas)*. The wing venation is like that of *Neorhaphiomidas* in the Apioceratidae but also shows some resemblance to that of the Mydaidae. The presence of short simple antennae and the rather short discal cell are perhaps indicative of the Apioceratidae. Genotype: *Megascelus nigricornis* Philippi.

Osten Sacken (1877) established the genus *Rhaphiomidas* for the Lower Californian *R. episcopus* and Coquillett (1892) described *Apomidas* for the Californian *A. trochilus*. The latter genus has insufficient characters to separate it from *Rhaphiomidas*, as will be shown, and is therefore placed as a synonym of that genus. Genotype: *Rhaphiomidas episcopus* Osten Sacken.

Hermann (1909) described the genus *Ripidosyrma* based on the South African species described by Melander (1907) as *Apiocera braunsi*. There is nothing in Hermann's description or in the figure and description given by Melander to indicate that the genus is distinct from *Apiocera*. The wing venation, two segmented palpi, terminalia, size, shape, pilosity, mouthparts, antennae and eyes are all characteristic of *Apiocera*. Therefore, the South African *A. braunsi* is here returned to *Apiocera*, where it was originally described by Melander, and the genus *Ripidosyrma* is placed as a synonym of *Apiocera*.

Norris (1936) proposed a new Australian genus *Neorhaphiomidas* and associated it only with the North American *Rhaphiomidas*, apparently being unaware of the Chilean *Megascelus* with which it also appears to be somewhat closely allied. The venation of the two genera is the same except that in *Megascelus* M3+4 continues to the wing margin. However, Norris (p. 64) states that in one female specimen of *Neorhaphiomidas* vein M3+4 is present, in addition to M2, as a small vein running out to the wing margin. Both genera apparently have sparsely pilose species of about the same size and shape. The palpi and ocelli were unfortunately not mentioned by Philippi. The two

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1 Schiner (1868) states that *Megascelus* is the same as the mydaid genus *Dolichogaster* Macquart. Gerstaecker (1868) excludes it altogether from the Mydaidae, recognizing it as a distinct family. Hunter (1901) includes *Megascelus* in the Mydaidae but footnotes conflicting viewpoints. Seguy (1938) places it as a synonym of *Dolichogaster* but gives no reason for this placement. The wing character used by Seguy, i.e., Cul + 1A not reaching margin, to key out *Dolichogaster* differs from the wing figure given by Philippi who shows this vein (M3 + 4) reaching the margin. It is, therefore, impossible to reach *Dolichogaster* with a specimen of *Megascelus*.

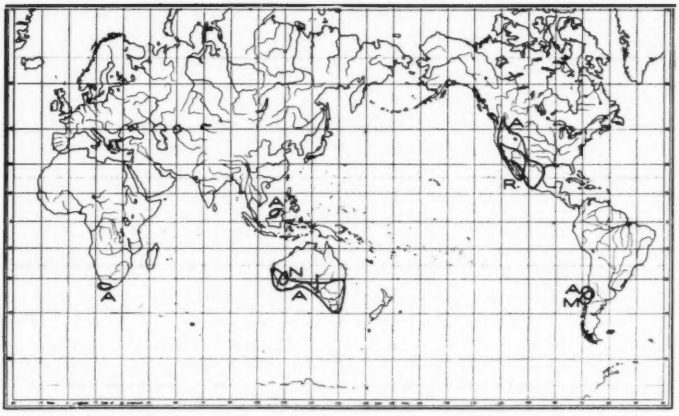

Fig. 1. World distribution of the family Apioceratidae. A = *Apiocera*, R = *Rhaphiomidas*, M = *Megascelus*, N = *Neorhaphiomidas*.

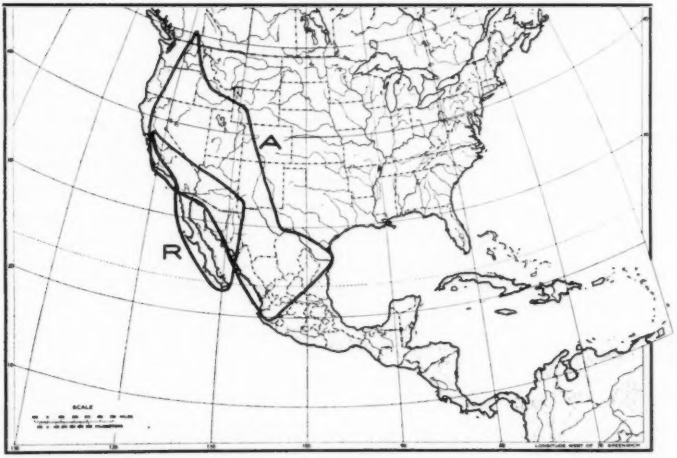

Fig. 2. Distribution of the family Apioceratidae in North America. A = *Apiocera*, R = *Rhaphiomidas*.

genera apparently differ in the shape of the terminalia, the extent of the mouthparts and the color. The presence of ocelli in *Neorhaphiomidas* will serve to separate them until further information is available and the genus will be retained. Genotype: *Neorhaphiomidas hardyi* Norris.

The family Apioceratidae is, therefore, composed of four genera, *Apiocera, Rhaphiomidas, Megascelus* and *Neorhaphiomidas;* the latter two genera are perhaps transitional forms between the Mydaidae and the more characteristic Apioceratidae.

Distribution

The family is rather widely but discontinuously distributed over much of the world, being represented in the Oriental, Australian, Ethiopian, Neotropical and Nearctic faunal realms. The type genus *Apiocera* has the most extensive distribution, occurring on the southern extremities of the Oriental, Australian, Neotropical and southwestern Nearctic regions (Fig. 1). The north-south range is from about 50 degrees north latitude in British Columbia to about 40 degrees south latitude in Tasmania and Chile.

The species have a marked preference for arid or semi-arid regions and are often taken either while resting on barren sandy ground, along unshaded streams, in open glades of the digger pine (upper Sonoran), and yellow pine-incense cedar (Transition) belts in California, or on flowers (lupines and sand verbenas) in the deserts of southern California. Thus far nothing is known about any of the immature forms except for the egg of an *Apiocera* as described by Norris (1936). This egg was deposited beneath the surface of the ground in a slightly moist place and was oval in shape and bright orange.

Apiocera, probably the most generalized and certainly the most polymorphic genus, occupies the entire area of distribution of the family, and although undergoing marked speciation within these widespread localities, has maintained its generic identity throughout. The species known at present from each of the regions are herein given. AUSTRALIA: *A. asilica* Westw., *A. brevicornis* (Wied.), *A. maerens* Westw.,[2] *A. deforma* Norris, *A. pica* Norris, *A. tonnoiri* Norris, *A. pallida* Norris, *A. minor* Norris, *A. newmani* Norris, *A. maritima* Hardy, *A. vulpes* Hermann. TASMANIA:[3] *A. Bigotti* (Macquart).[4] BORNEO: *A. maerens* Westw. CHILE: *A. obscura* (Philippi), *A. philippii* (Brethes). NORTH AMERICA: *A. augur* O. S., *A. haruspex* O. S., *A. bilineata* Painter, *A. trimaculata* Painter, *A. interrupta* Painter, *A. aldrichi* Painter, *A. clavator* Painter, *A. martinorum* Painter, *A. beameri* Painter, *A. convergens*

2 The identity of several of these early species is questionable and the synonymy of the Australian species has yet to be worked out satisfactorily.

3 Hardy (1933) questions this locality, stating that the genus is not known from there.

4 In 1854, Walker placed *A. Bigotii* as a synonym of *A. asilica* Westw. but the description given by Walker was that of *A. maerens* Westw. and not of *A. asilica.* It is possible that Walker intended to make Macquart's species a synonym of *A. maerens* (Hardy, 1921).

Painter, *A. notata* Painter, *A. caloris* Painter, *A. pearcei* Cazier, *A. alleni* Cazier, *A. parkeri* Cazier, *A. exta* Cazier, *A. hispida* Cazier, *A. intonsa* Cazier, *A. melanura* Cazier, *A. infinita* Cazier. AFRICA: *A. braunsi* Melander.

Megascelus appears to be endemic in Chile and is represented by a single species, *M. nigricornis* Philippi. This genus has not been treated in the literature dealing with this family (except by Brues and Melander, 1932) in spite of the fact that it seems to offer definite clues to the relationships of certain genera within the family as will be pointed out later.

Neorhaphiomidas is endemic in Australia and is represented by two species, *N. hardyi* Norris and *N. pinguis* Norris.

Rhaphiomidas is endemic in North America and is apparently confined to the arid and semi-arid regions of southwestern United States (California, Arizona and New Mexico) and to Lower California, Mexico. Additional collecting will undoubtedly prove its presence in northern Mexico, Utah and Nevada. The species known at present are *R. trochilus* (Coq.), *R. episcopus* O. S., *R. acton* Coq., *R. xanthos* Townsend, *R. terminatus* Cazier, *R. painteri* Cazier, *R. aitkeni* Cazier, *R. abdominalis* Cazier, *R. maehleri* Cazier, *R. maculatus* Cazier and *R. parkeri* Cazier. Like many other animals and plants in this area its nearest apparent relatives are found in Chile. Osten Sacken (1877) associated it with the Chilean *Mitrodetus* Gerst. (Mydaidae).[5]

That the family is archaic is hardly to be denied when one considers the discontinuous peripheral distribution of the genus *Apiocera*, (Fig. 1), and the continental isolation and evolution of *Megascelus*, *Rhaphiomidas* and *Neorhaphiomidas* as genera distinct from *Apiocera*. Certain morphological characters of family value in many Diptera assume a role of generic or specific (or less) importance in the Apioceratidae, especially in the southern extremities of the distribution. This feature probably indicates that the group is very old and, further, when the small number of species and the relative scarcity of most forms is considered, it does not seem unreasonable to assume that the family is undergoing decadence. This same situation is also found, to a similar degree, in the Mydaidae and Nemestrinidae. The Asilidae and Therevidae, on the other hand, appear to be less archaic and hence are more difficult to associate phylogenetically with the Apioceratidae.

At the present time nothing is known concerning the geological history of the family but it seems reasonable to speculate that this additional source of information will eventually be forthcoming since there are a number of fossil Nemestrinidae known from the Miocene deposits of Florissant, Colo-

5 "Closely allied to *Mitrodetus* Gerstaecker as there are three cells intervening between the forked cell and the margin of the wing, and as the structure of the proboscis is the same, long and linear, directed forward, with very narrow lips at the end; differing, however, from that genus in the structure of the antennae, in some minor characters of the venation, among them the structure of the second submarginal or forked cell, which is petiolate at the proximal end only, and not at both ends; and in the presence of two distinct ocelli."

rado.[6] The present distribution of the nemestrinids would indicate that they have had a geological history similar to that of the Apioceratidae, being perhaps somewhat more plastic and biotypical and therefore exhibiting a larger and more continuous distribution.

Phylogeny

Gerstaecker (1868) left the members of this family more or less unassociated; Philippi (1865), Osten Sacken (1883) and Macquart (1838) placed them in the Asilidae; Schiner (1868) and Osten Sacken (1878) placed them in the Mydaidae, and Coquillett (1885) placed them in the Therevidae. They were treated as a distinct family allied to the Mydaidae and Therevidae by Brauer (1882); as a family allied to the Therevidae by Macquart (1846), Mik (1884 and 1890) and Brues and Melander (1932); as a family allied to the Mydaidae and Nemestrinidae by Westwood (1841); as a separate family under "Asilides" by Bigot (1857); as a separate family allied to the Asilidae and Mydaidae by Williston (1888 and 1893), Kertesz (1909), Imms (1929); as a family between the Therevidae and Bombyliidae by Curran (1934); as a family between the Therevidae and Asilidae by Essig (1929); as a family between the Mydaidae and Bombyliidae by Comstock (1904); as a family between the Mydaidae and Dolichopodidae by Comstock (1930) and as a family allied to the Therevidae on the one hand and the Asilidae and Mydaidae on the other by Hermann (1909).

The lack of pertinent additional facts makes a definite conclusion as to the relationships of the family impossible at the present time; however, an examination of the above arrangements and the more important papers by Williston, Osten Sacken and Hermann indicate a rather close relationship with the Asilidae, Mydaidae and perhaps the Therevidae. The discussion to follow tends to strengthen the placement near the Mydaidae and is based on some of the more important morphological characters. The group is generally recognized today as being of family rank, although Hardy (1934) intimates that they may be nothing more than another subfamily of the Asilidae. The discovery of the larval forms of any member of the family will undoubtedly assist in solving this phylogenetic enigma.

A discussion of the phylogeny of the genera which constitute this family is particularly hazardous at this time since the ancestry of the family is uncertain. However, one cannot gather information concerning a group without formulating some idea as to its relationships. The following discussion is presented with the understanding that the evidence is as yet rather incomplete and that future workers will undoubtedly bridge many of the gaps in our present knowledge.

In any discussion of phylogeny it is necessary and practical that only the most fundamental indicative morphological characters be used, that is, those characters which reflect group stability but allow for correlation with other

6 Bequart, J. C. and F. M. Carpenter. 1936. Jour. of Paleo. (5) **10**:395-409.

groups. For instance, in the genus *Apiocera* there is relative uniformity in the extent of terminalia development even though these structures show specific characteristics and a trend toward other families. The wings are relatively stable for each genus and offer one of the best characters for consideration. The development of the palpi likewise appears to be of some significance. The remainder of the characters are, for the most part, too variable or too little known to be considered here. In the genera *Megascelus* and *Neorhaphiomidas* the ocelli offer an additional character.

Wings.—One of the fundamental studies of the phylogeny of a single dipterous family, as based on wing characters, is that of C. P. Alexander (1927) on the Tipulidae. In this paper the movement and interpretation of the veins is discussed in a highly enlightening manner, and a phylogenetic tree is constructed. The main thesis of this paper will be adhered to in the following discussion.[7]

For a satisfactory treatment of the progressive development of various vein positions and the direction of specialization in the Apioceratidae, it is necessary to seek a more simplified form (or forms) in a related group, that will aid in explaining the progressive translocation of veins. The present discussion will begin with several genera of Asilidae which appear to offer a logical sequence in the development of the vein positions in the Apioceratidae. *Echtopoda pubera* Loew (Plate 1, Fig. 1) has a full complement of veins (Alexander, 1927) reaching the margin except that R2 and R3 are fused. *Ceraturgus cruciatus* Say (Plate 1, Fig. 2) is essentially the same as *Echtopoda* except that Cu1 and 1A are now narrowly united. In the genus *Laphystia* (Plate 1, Fig. 3) the appearance is much the same except that R2+3 has migrated basally and is now attached to R1 close to the costal margin thus closing cell R1; M3 and M4 are fused apically closing cell M3.

The wing of *Apiocera infinita* Cazier (Plate 1, Fig. 4) shows a further migration of R2+3 basally on R1; R4 has migrated toward R1 leaving cell R2+3 narrowly open; R5 and M1 have migrated to the costal margin and M2 is extending in that direction but is still on the posterior margin. This means that a radical change in the veins R4, R5 and M1 has taken place between this genus and *Laphystia*.[8] *In Rhaphiomidas acton* Coq. (Plate 1, Fig. 5) the only vein to undergo major translocation is M2 which is now connected above the wing apex on the costal margin, R4 may or may not terminate on R1 and R5 and M1 are crowded basally but not sufficiently to close their respective cells. The magnitude of the change between these two genera is obviously much less than that between *Apiocera* and the asilid *Laphystia*.

If the genera *Megascelus* and *Neorhaphiomidas* were to be considered at

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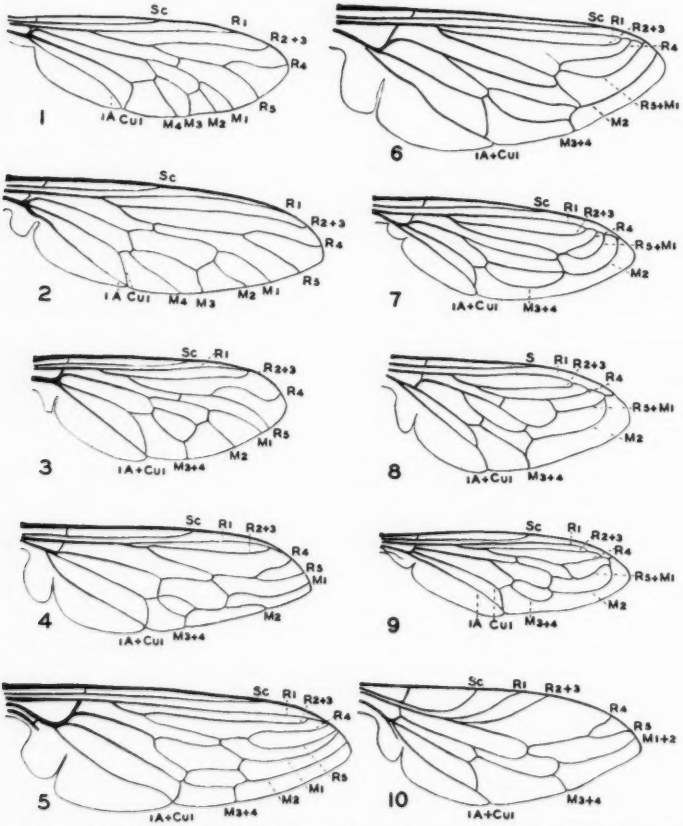
7 It is of interest, in connection with Alexander's paper, to note the appearance of vein R2 as a cross vein between R3 and R1 in the wing of the asilid, *Laphria sicula* McAtee (Plate 4, Fig. 18).

8 *Apiocera maritima* Hardy (Plate 1, Fig. 10) has a wing unlike any other species in the family. Veins M1 and 2 are united as are M3 and 4 and all veins except Cu1 reach the margin of the wing, M1 and 2 extending to the anterior margin.

this point one would be impressed with the fact that they are as different from *Apiocera* and *Rhaphiomidas* in specialization as are the asilid genera in generalization. However, by the interpolation of two mydaid wings this difference becomes less abrupt and the sequence more logical. In the genus *Mydas* (Plate 1, Fig. 6) there is a further migration of R2+3 and R4 basally on R1, R5 and M1 are now united and terminate on R1 thus closing cell R4. The discal cell is more elongate and Cu1 meets 1A more toward the base. Further migra-

PLATE 1



Wings of 1. *Echtopodo* pubera Loew. 2. *Ceraturgus cruciatus* Say. 3. *Laphystia* n.sp. 4. *Apiocera infinita* Cazier. 5. *Rhaphiomidas acton* Coquillett. 6. *Mydas* sp. 7. *Nemomydas* sp. 8. *Megascelus nigricornis* Philippi. 9. *Neorhaphiomidas hardyi* Norris. 10. *Apiocera maritima* Hardy.

tion takes place in the genus *Nemomydas* Curran (Plate 1, Fig. 7) where M2 is in contact with R1 and cell R5+M1 is therefore closed. In this genus the marginal connection of M3+4 is lacking just as it is in one of the following genera.

The differences between *Megascelus* (Plate 1, Fig. 8) and the mydaid group are less pronounced than those between *Apiocera* and *Laphystia* (Asilidae), the only major changes being in the connection of M2 with R5+M1 and in the reappearance of M3+4 at the margin in *Megascelus*. Neorhaphiomidas (Plate 1, Fig. 9) is the same as *Megascelus* except that M3+4 is absent in most specimens (not all), and cell R5 appears to be more elongate and narrowed and is not distorted along cell R5+M1.

After a consideration of these wing differences it is evident that the family lends itself to a somewhat natural division. *Apiocera* and *Rhaphiomidas* form a group rather distantly related to the Asilidae and somewhat more closely to the Mydaidae. *Megascelus* and *Neorhaphiomidas*, on the other hand, form a group rather closely allied in this character to the Mydaidae and less so to the *Apiocera-Rhaphiomidas* group.

Terminalia.—These structures present additional evidence to support that offered by the wings. In both *Apiocera* and *Rhaphiomidas* they are greatly enlarged, especially in the latter, and, although distinct, resemble somewhat those of *Erax* and *Promachus* in the Asilidae. The terminalia of *Neorhaphiomidas* and *Megascelus*, on the other hand, are very small and somewhat retracted within the abdomen as they are in the mydaid genera *Nemoneura* Bezzi and *Nemomydas* Curran. The morphological equivalents require further study.

Palpi.—These structures are well developed in *Apiocera* and *Rhaphiomidas*, being two-segmented in the former and one-segmented in the latter. In *Neorhaphiomidas* and probably *Megascelus* (not described by Philippi) they are very short, reduced and one-segmented. The Mydaidae are characterized by having the palpi absent or very small and one-segmented and thus appear to be most closely allied to the *Megascelus-Neorhaphiomidas* group. In the Asilidae the palpi are rather well developed and two-segmented, suggesting an affinity with *Apiocera*.

Ocelli.—The presence of three ocelli in *Apiocera* and *Rhaphiomidas* again appears to substantiate the asilid association. However, *Neorhaphiomidas* also has three, whereas *Megascelus*, judging from the description, lacks them. This would favor the inclusion of *Neorhaphiomidas* with the *Apiocera* since the Mydaidae lack ocelli or have, at most, only one ocellus.

Antennae.—These structures appear to separate all four genera from the Mydaidae because of their three- rather than four-segmented condition. The asilids generally have three-segmented antennae but sometimes may have more.

Mouthparts.—The various structures here show a rather close relationship with those in the Mydaidae and less so with the Asilidae. In the Asilidae the labella is immovable and is without pseudotracheae, whereas in the Apiocerati-

dae it is rather broad and movable and is equipped with pseudotracheae. These differences are correlated with the food habits of each family and are, perhaps, of secondary importance in this discussion.

Summary

Judging from the facts presented it appears that there are two rather divergent groups within the Apioceratidae sufficiently separated to be called subfamilies. The Apioceratinae comprising *Apiocera* and *Rhaphiomidas* and the Megascelinae[9] to include *Megascelus* and *Neorhaphiomidas*. The group Apiocerinae was originally proposed by Williston (1893) and restricted to *Apiocera* but is here enlarged as Apioceratinae to include *Rhaphiomidas* (Rhaphiomidinae of Williston).

Within the Apioceratinae the genus *Apiocera* appears to be the generalized stock, possibly arising from an asilid-like ancestor, from which *Rhaphiomidas* was derived. The former genus is more widely distributed, has two palpal segments rather than one, more primitive wing venation and terminalia and less highly modified mouthparts. In the Megascelinae the genus *Neorhaphiomidas* appears to link *Megascelus* with the Apioceratinae and also shows certain affinities for the Mydaidae. Perhaps the Mydaids are an offshoot from an apioceratid-like ancestor. There are, however, numerous objections to the latter assumption and it is far from proven correct.

The nemestrinids appear to be more distantly related to the Apioceratidae and can be separated from them by the presence of the diagonal vein in the wing (a composite vein made up of the base of R2+3, R4+5, radial medial cross vein, median portion of M1, M2 and apex of M3+4), by having R2+3 parallel and not connected with R1. The lack of macrochaetae (eremochaetous) and the presence of a pulvilliform empodium in the nemestrinids also serve to distinguish the two. The nemestrinid antennae are three-segmented with terminal style arista-like, three-segmented and bare and the ovipositor is long.

KEY TO THE GENERA OF THE FAMILY APIOCERATIDAE

1. Cells R5 and M1 open, veins R5 and M1 not united apically, M2 not terminating on R5 or M1 (Plate 1, Figs. 4 and 5); male terminalia enlarged, lateral lobes of ninth sternite and tergite well developed and large. (Apioceratinae)..... 2

   Cells R5 and R5 + M1 closed, veins R5 and M1 united distally, M2 terminating on R5 + M1 (Plate 1, Figs. 8 and 9); male terminalia small, lateral lobes of ninth sternite and tergite present but small. (Megascelinae). 3

2. Palpi two-segmented; gonostyles ventro-lateral in position; conical swellings absent from lateral lobes of postnotum. .....*Apiocera* Westwood

   Palpi one-segmented; gonostyles ventral in position; large conical swellings present on lateral lobes of postnotum. .....*Rhaphiomidas* Osten Sacken

3. Head with vertex convex; ocelli three in number. .....*Neorhaphiomidas* Norris
   Head with vertex concave; ocelli absent(?). .....*Megascelus* Philippi

9 No specimens of this subfamily were available to the writer, their characteristics were taken from Norris (1936) and Philippi (1865).

Genus APIOCERA Westwood

Apiocera Westwood, 1835, Lond. and Edinb. Phil. Mag. and Jour. Sci., (3) **6**:448; Macquart, 1840, Dipteres Exotiques Nouveaux ou peu connus, (2) **1**:397; Westwood, 1841, Arcana Entom., **1**:56; Bigot, 1857, Ann. Ent. Soc. France, **26**:537; Gerstaecker, 1868, Stett. Ent. Zeit., **29**:70; Osten Sacken, 1877, Bul. U. S. Geol. and Geog. Surv. of the Territories, **3**:283-284; Osten Sacken, 1878, Wash. Smith. Misc. Coll., 2nd. Ed., p. 85; Osten Sacken, 1883, Berliner Ent. Zeit., **27**:287-294; Mik, 1884, Wien. Ent. Zeit., **3**:27; Coquillett, 1885, Psyche, **4**:243-244; Osten Sacken, 1886, Berliner Ent. Zeit., **30**:138; Williston, 1888, Psyche, **5**:99-102; Williston, 1888, Synopsis of the Families and Genera of North American Diptera, p. 32; Osten Sacken, 1891, Berliner Ent. Zeitsch., **36**:421; Osten Sacken, 1891, Berliner Ent. Zeitsch., **36**:311-315; Williston, 1893, Kansas Univ. Quart., (3) **1**:101-118; Osten Sacken, 1902, Biologia Cent. Amer., **1**:212-213; Melander, 1907, Bul. Wisc. Nat. Hist. Soc., **5**:125-127; Williston, 1908, Manual of North American Diptera, 3rd. Ed., p. 188-189; Hermann, 1909, Deutsch. Ent. Zeitschr., Beiheft, **1909**: 104-122; Coquillett, 1910, Proc. U. S. Nat. Mus., **37**:499; Hardy, 1921, Proc. Linn. Soc. N. S. W., **46**:297-298; Brethes, 1924, Rev. Chil. Hist. Nat., **28**:104; Painter, 1932, Ann. Ent. Soc. Amer., (2) **25**:350-357; Hardy, 1933, Proc. Linn. Soc. N. S. W., **58**:416; Hardy, 1934, Ann. Mag. Nat. Hist., (10) **13**(77):505; Norris, 1936, Jour. Royal Soc. West. Australia, **22**:49-70; Painter, 1936, Bul. Univ. Kans., **37**:187-203; Curran, 1934, The Families and Genera of North American Diptera, p. 189-190.

Tapinocera Macq., 1838, Dipt. Exot., (2) **1**:78. Type, *Laphria brevicornis* Wied.

Pomacera Macq., 1846, Dipt. Exot., Suppl. **2**:63. Type, *Laphria brevicornis* Wied.

Anypenus Phil., 1865, Verh. Zool.-Bot. Gesellsch. in Wien, **15**:702; Brethes, 1924, Rev. Chil. Hist. Nat., **28**:104. Type, *Anypenus brevicornis* Phil. = *Apiocera philippii* Brethes.

Ripidosyrma Hermann, 1909, Deutsch. Ent. Zeitsch., 104 *(New Synonym)*, type, *Apiocera braunsi* Melander.

Medium sized, narrow, large-headed, setigerous, thinly pilose flies. *Head* with compound eyes rather widely separated, slightly narrowed in the male, vertex with three ocelli; antennae three-segmented, terminal style one or indistinctly two-segmented; palpi prominent, two-segmented; mouthparts generally short and with well defined labella. *Thorax* well developed, mesonotum with setae on sides and posterior margins; scutellum well developed, setigerous. *Wings* (Plate 1, Fig. 4) with R4, R5 and M1 curved anteriorly, terminating on costal margin,[10] M2 terminating on posterior margin, discal cell short. *Abdomen* gradually tapering apically legs long and slender, not fitted for grasping, empodia lacking. *Terminalia* (Plate 4) rather complex, well developed; lateral lobes of ninth tergite, ninth sternite and gonostyles forming a box-like enclosure for genital and anal organs; interbasal fold well developed, variously ornamented and lying within concavity of basistyle; parameres well developed, variously shaped, occurring lateral to and in contact with the penis valves and appearing to aid in guiding the latter structure; penis valves situated lateral to round, pointed, sclerotized penis, generally with dorsal bridge and flap-like lateral pieces in contact with parameres, apices open ventrally and forming a slot through which the penis projects; proctiger dorsal, sclerotized basally, membranous and trilobed apically; lateral lobes of ninth tergite with

10 The Australian *A. maritima* Hardy has M1 and M2 united and terminating on costal margin (Plate 1, Fig. 10). This cannot, however, be confused with *Rhaphiomidas* as the discal cell is absent due to this fusion.

varying types and degrees of sculpturing on inner concave surface, usually with apical inner fold.

Genotype: *Apiocera fuscicollis* West. =*Apiocera brevicornis* (Wied.), vide Hardy (1933), Coquillett designation, 1910.

Type locality.—Australia (probably New South Wales, Hardy 1933).

This genus is distinct among the Nearctic Apioceratidae because of its relatively small size, narrow form, abbreviated mouthparts, two-segmented palpi and by the wing venation (Plate 1, Fig. 4). The absence of the conical swellings on the lateral lobes of the postnotum and the more complex terminalia development also serve to distinguish it from *Rhaphiomidas*.

These structures appear to be relatively constant in all the Nearctic species but are known to undergo variation in some of the Australian forms (Hardy, 1933; Norris, 1936). The mouthparts are much more elongate and variable in some of the Australian species than in the Nearctic forms which show little if any variation in this structure. The length of the antennae is also variable in the Australian forms and, except for small differences in the shape of segments, is relatively constant in the Nearctic species. In the latter species little variation is found in the wing venation. Hardy (1933) records considerable variation in the veins of the Australian *A. maritima* Hardy which sometimes has R4, R5 and M1 shortened or even absent. The terminalia form one of the most consistent characters in both regions but appear to vary in different ways. Norris (1936) figures side views of the lateral lobes of the ninth tergite and sternite to show the specific differences, whereas, in the Nearctic forms the greatest external differences are, for the most part, on the ninth sternite and gonostyles. The genitalic organs which are within the box-like outer structures offer many additional specific characters but are not treated in detail in this paper. It is hoped that when adequate *Apiocera* material is available that it will be possible to make a detailed study of these organs. The nomenclature used in the brief discussion above was adopted from Freeborn (1924).

The more important characters of use in differentiating Nearctic species, aside from the terminalia, include: color and extent of pile and macrochaetae on various portions of the body, pigmentation and maculation. It is admitted that some of these structures are variable, but when used in conjunction with the terminalia they aid greatly in defining species.

The writer would like to acknowledge the guidance obtained from the excellent revision of the genus *Apiocera* published by R. H. Painter (1936). The key is adopted and modified from that given by Painter so as to include the new species and several variations observed in previously described forms. The females are more difficult to separate than the males and, at the present time, the sexes are inadequately correlated in many species, thus, making it impossible to present a complete key to this sex. The incomplete female key given will aid, for the most part, only in grouping the females into major groups.

Key to the Species of Apiocera in North America

MALES

1. Pteropleura (mesanepimera) with a more or less conspicuous tuft of rather long hair in front of the metathoracic spiracles. 2
   Pteropleura (mesanepimera) bare or uniformly short pilose or pollinose in front of the metathoracic spiracles. 10
2. Dorso-caudal angle of mesopleura (mesanepisterna) with strong macrochaetae in addition to hair. 3
   Dorso-caudal angle of mesopleura (mesanepisterna) without macrochaetae, generally with tuft of white hair. (also *A. martinorum* Painter). ..... *trimaculata* Painter
3. Thoracic dorsum with pile black or brown; macrochaetae of body and legs largely black. 4
   Thoracic dorsum with pile white; macrochaetae of body and legs largely white. ..... *caloris* Painter
4. Middle portion of ninth sternite slender, extending to apical third of ninth hemitergites and even with or beyond transverse portions of interbasal folds (Plate 4, Fig. 6) ..... *alleni* Cazier
   Middle portion of ninth sternite broad, not extending posteriorly beyond middle of ninth hemitergites and not beyond transverse portions of interbasal folds. (Plate 4, Figs. 1-5) 5
5. Terminalia with pile white except on base of hemitergites, long. (Plate 4, Fig. 17) ..... *hispida* Cazier
   Terminalia with pile black, short. 6
6. Compound eyes separated from lateral ocelli on vertex by less than width of a lateral ocellus. 7
   Compound eyes separated from lateral ocelli on vertex by the width or more than width of a lateral ocellus. ..... *parkeri* Cazier
7. Lateral lobes of ninth tergite (hemitergites) without deep subapical notch on inner margin; outer margin with large shallow apical notch. 8
   Lateral lobes of ninth tergite (hemitergites) with deep subapical notch on inner margin (Plate 4, Fig. 16). ..... *aldrichi* Painter
8. Terminalia with transverse projections of interbasal folds projecting prominently into ventral opening. 9
   Terminalia with transverse projections of interbasal folds not projecting into ventral opening (Plate 4, Fig. 2) ..... *exta* Cazier
9. Median projection of ninth sternite overlapping laterally gonostyles for more than two-thirds length of median projection (Plate 4, Fig. 3); palpi with terminal segment brown at most on proximal half. ..... *pearcei* Cazier
   Median projection of ninth sternite not overlapping laterally gonostyles beyond middle of median projection (Plate 4, Fig. 4); palpi with terminal segment dark brown throughout. ..... *beameri* Painter
10. (1) Dorso-caudal angle of mesopleura with three or four strong black macrochaetae. (also *A. augur*). ..... *clavator* Painter
    Dorso-caudal angle of mesopleura bare or slightly hairy. 11
11. Dististyles of terminalia with a subapical flare of long hair (Plate 4, Fig. 15). ..... *intonsa* Cazier
    Dististyles of terminalia without a subapical flare of bicolored hair. 12
12. Macrochaetae on femora and tibiae of legs mostly white or yellowish. 13
    Macrochaetae on femora and tibiae of legs mostly black. 16
13. Terminalia light reddish-brown in color; pile on terminalia predominantly white or yellowish apically. 14
    Terminalia piceous in color; pile on terminalia predominantly black apically. 15
14. Abdominal spots convex above, straight below; pulvilli usually more than half as long as claws. ..... *interrupta* Painter

Abdominal spots quadrate; pulvilli small, about half as long as claws. ..... *bilineata* Painter

15. (13) Lateral abdominal spots prominently convex above, straight below, spots widely interrupted between segments. ..... *melanura* Cazier
Lateral abdominal spots quadrate, occasionally with upper surface of markings on basal three segments shallowly convex, spots, scarcely interrupted between segments, forming an almost continuous black band (Plate 3, Fig. 6). ..... *infinita* Cazier

16. (12) Dorsum of abdominal segments three and four broadly black. 17
Dorsum of abdominal segments three and four with dark spots. 18

17. Ninth tergite notched at apex, terminalia piceous. ..... *haruspex* Osten Sacken
Ninth tergite not notched at apex, terminalia black. ..... *notata* Painter

18. (16) Abdominal markings triangular and lateral in position, not extending across dorsum, sometimes almost lacking or confined to two small triangular spots on segments two and three. ..... *augur* Osten Sacken
Abdominal markings either subquadrate spots or lateral black stripes constricted or interrupted at the base or apex of segments three and four. 19

19. Lateral lobes of ninth tergite notched at apex; abdomen with central black stripe and lateral black stripes constricted or interrupted at the base or apex of segments three and four. ..... *martinorum* Painter
Lateral lobes of ninth tergite not notched at apex; abdomen with two white stripes extending entire length, breaking the black areas into dorsal and lateral spots. ..... *convergens* Painter

FEMALES

1. Pteropleura (mesanepimera) with a more or less conspicuous tuft of rather long hair in front of the metathoracic spiracles. 2
Pteropleura (mesanepimera) bare or uniformly short pilose or pollinose in front of the metathoracic spiracles. 5

2. Abdominal segments with retrorse hairs largely white on segments five, six and seven. ..... *beameri* Painter
Abdominal segments with at least retrorse hairs on segments six and seven black. 3

3. Abdominal segments six and seven only with black retrorse hairs. ..... *caloris* Painter; *pearcei* Cazier
Abdominal segments with retrorse black hair on segments four or five in addition to six and seven. 4

4. Abdominal segments four to seven with black retrorse hairs. ..... *aldrichi* Painter
Abdominal segments five to seven with black retrorse hairs. ..... *parkeri* Cazier

5. (1) Abdominal segments four to seven with retrorse hair white or yellowish. ..... *bilineata* Painter; *interrupta* Painter
Abdominal segments five to seven with retrorse hair black. 6

6. Setae of body largely white; abdomen with subtriangular spots laterally on segments two and three, indistinct on four. ..... *martinorum* Painter; *augur* Osten Sacken
Setae of body largely black; abdomen with subquadrate lateral spots on segments two, three and four, distinct on four. ..... *haruspex* Osten Sacken; *convergens* Painter; *notata* Painter

The females of *A. trimaculata* Painter, *A. clavator* Painter, *A. alleni* Cazier, *A. intonsa* Cazier, *A. infinita* Cazier, *A. melanura* Cazier, *A. exta* Cazier and *A. hispida* Cazier are as yet unknown.

Apiocera trimaculata Painter

Apiocera trimaculata Painter, 1936, Bul. Univ. Kans., **37**·195-196.

Medium sized, rather slender; macrochaetae white except on tarsi; densely

clothed throughout with white pile; abdomen with diamond-shaped dorsal black spots on segments two, three and four; terminalia brownish, white pollinose and pilose (Plate 4, Fig. 1). Length 17 mm.

Type locality.—San Diego County, California.

Most closely allied to *A. caloris* Painter but distinguishable by the terminalia.

Apiocera caloris Painter

Apiocera caloris Painter, 1936, Bul. Univ. Kans., **37**:194-195.

Medium sized, rather slender; macrochaetae, pollen and pile white; abdominal segments two, three and four with central brown or blackish spots, spots on segments three and four covering most of dorsum; terminalia brown, white pilose (Plate 4, Fig. 3). Length 18 mm.

Type locality: Tinajas Atlas, Yuma County, Arizona, 1905.

Allied to *A. aldrichi* Painter but easily separated by the abdominal maculations and the terminalia.

Apiocera beameri Painter

Apiocera beameri Painter, 1936, Bul. Univ. Kans., **37**:198-199.

Large, robust; macrochaetae of head white, of coxae mostly white, black on thorax, femora and tibiae; abdomen with segment one brownish in center and along posterior margin, segment two brownish on anterior border and with black crossband expanded broadly in center to the posterior border and also laterally, remainder of dorsum white, segment three mostly black, anteriolateral and posteriolateral margins brownish, segment four black with anterior margin narrowly brownish and posterior margin white, segments five, six and seven mostly white; terminalia piceous, pile black (Plate 4, Fig. 4). Length 22 mm.

Type locality: Cuyama Ranch, Santa Barbara County, California, July 25, 1935.

Closely allied to *A. aldrichi* Painter but easily separated by the different abdominal pattern in the male and the terminalia.

Apiocera pearcei n. sp.

Male.—Large, robust. Mesonotal hair brown, abdominal hair beneath white; macrochaetae black throughout. Abdominal segments one through four with dorsal black markings; terminalia piceous, pile black. Pteropleura with tuft of white hair in front of metathoracic spiracles. Dorso-caudal angle of mesopleura with tuft of white hair and three strong black macrochaetae. Compound eyes separated from lateral ocelli on vertex by less than width of a lateral ocellus. *Head* with white pollen and pile on front; antennae white pollinose and pilose, first segment dark, second segment reddish-brown, third segment predominantly black. *Mesonotum* brown pollinose, macrochaetae black. *Abdomen* white pollinose, pile on dark areas black; second segment with black dorsal spot on basal portion oblong, median triangular area extending posteriorly;

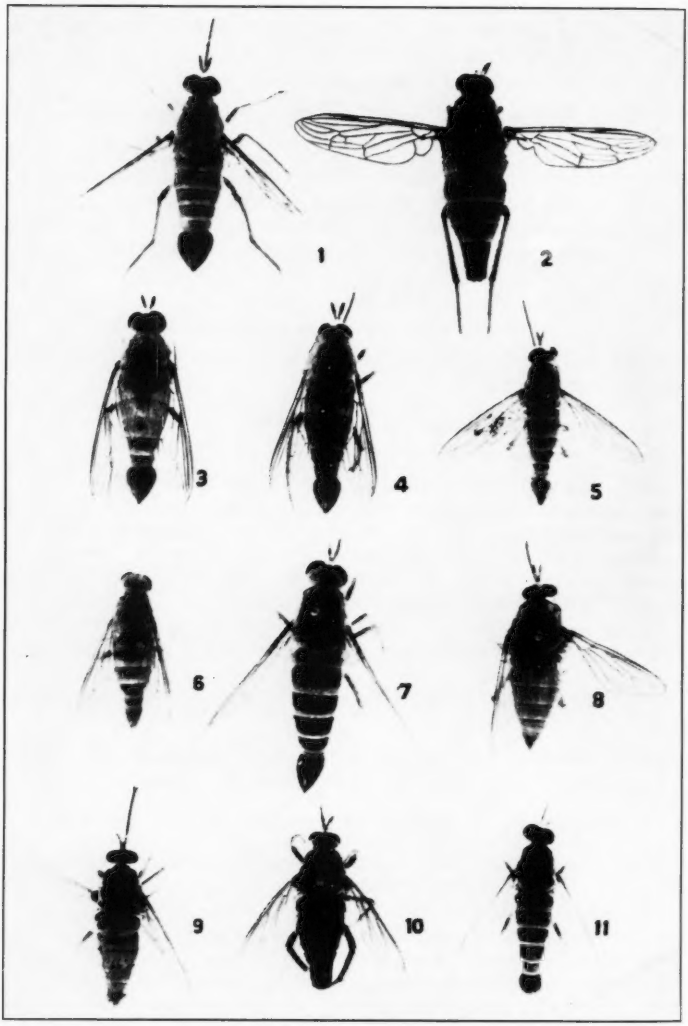


PLATE 2: Figs. 1, 3-11. Males of *Rhaphiomidas* species. 1, *R. acton* Coquillett. 2, Female of *R. acton* Coquillett. 3, *R. maehleri* Cazier. 4, *R. maculatus* Cazier. 5, *R. abdominalis* Cazier. 6, *R. aitkeni* Cazier. 7, *R. trochilus* (Coquillett). 8, *R. xanthos* Townsend. 9, *R. painteri* Cazier. 10, *R. episcopus* Osten Sacken. 11, *R. parkeri* Cazier.

third and fourth segments with median triangular area, apex anterior; terminalia with median portion of ninth sternite wide and membranous, not extending to transverse projections of interbasal folds, lateral lobes of ninth tergite with shallow apical impression (Plate 4, Fig. 3). *Legs* with femora black, tibiae and tarsi reddish-brown; pulvilli about three-fourths length of claws. Length 20 mm., width 4 mm. (Plate 3, Fig. 3).

Female.—Similar to male but without macrochaetae on the dorsocaudal angle of mesopleura; abdomen with small black spots laterally on segments two and three, segments four and five with retrorse white pile, segments six and seven with retrorse black pile; occasional macrochaetae white. Length 18 mm., width 4 mm.

Holotype male in the writer's collection, taken at Phelan, San Bernardino County, California, June 26, 1937 (K. L. Maehler); allotype female also in the writer's collection, taken at Yermo, San Bernardino County, California, July 14, 1939, by W. M. Pearce after whom the writer takes pleasure in naming the species. Two imperfect male specimens from Yermo studied.

Apiocera pearcei appears to be closely allied to both *Apiocera aldrichi* Painter and *Apiocera caloris* Painter. It can be distinguished from *A. aldrichi* by the triangular markings on abdominal segments three and four, by the wider and more membranous median projection of the ninth sternite, by the prominent lateral projections of the interbasal folds and by the lack of incisions in the inner apical margins of the lateral lobes of the ninth tergite. From *A. caloris* it can be distinguished by the brown mesonotal hair, by the black macrochaetae, by its larger size, by the black pile and piceous color of the terminalia and by its more closely placed compound eyes. The terminalia of *A. pearcei* and *A. caloris* are structurally very much alike on the exterior.

Apiocera aldrichi Painter

Apiocera aldrichi Painter, 1936, Bul. Univ. Kans., **37**:193-194.

Large, robust; macrochaetae predominantly black, pile mostly white; abdominal segments two, three and four with large, black transverse bands, area anterior to bands grey, posteriorly white, pile on black markings of segments three and four black; terminalia piceous, pile black (Plate 4, Figs. 5 and 16). Length 21-23 mm. (Plate 3, Fig. 1).

Type locality: Yuma, Yuma County, Arizona, June 26, 1917. Additional localities include: Riverside County, San Bernardina County, Los Angeles County, San Diego County, and Imperial County in California and Yuma County, Maricopa County, Coconino County and Pinal County in Arizona.

A rather large, densely pilose species closely allied to the preceding species and to *A. hispida* Cazier but distinguishable by its terminalia, abdominal markings and pilosity.

Apiocera hispida n. sp.

Male.—Large, robust. Mesonotal hair brown; scutellar hair white; abdominal hair throughout white, long; macrochaetae black except for few on legs. Abdominal segments one through four with dorsal black markings; terminalia

piceous, pile white except at extreme base of lateral lobes of ninth tergite. Pteropleura with tuft of white hair in front of metathoracic spiracles. Dorso-caudal angle of mesopleura with tuft of white hair and one strong seta. Compound eyes separated from lateral ocelli on vertex by the width of a lateral ocellus. *Head* white pollinose, pile on vertex black, front white pilose; antennae white pollinose and pilose, all segments black. *Mesonotum* brown pollinose, macrochaetae black. *Abdomen* white pollinose, pile on dorsum (including dark areas) of segments one, two and three half as long as width of segments, white; first segment black dorsally except for narrow basal and apical white bands; second segment with median, wide, transverse black band; third and fourth segments with wide black basal bands, extending beyond middle of segments, not reaching pleurae laterally; segments five, six and seven uniformly white pollinose; segment eight brown; terminalia robust, similar to that of *A. aldrichi* Painter but more blunt, subapical notch very shallow, apical notch wide and shallow (Plate 4, Fig. 17). Legs with femora black, tibiae and tarsi reddish-brown; pulvilli about three-fourths length of claws. Length 22 mm., width 4.8 mm. (Plate 3, Fig. 2).

Female.—Unknown.

Holotype male in the writer's collection, taken at Yermo, San Bernardino County, California, May 23, 1940, by W. Reeves, P. C. Ting, and M. Cazier.

Apiocera hispida is most closely allied to *A. aldrichi* Painter and *A. alleni* Cazier. It can be distinguished from *A. aldrichi* by the white pile on the terminalia, by the long white pile on the dorsal black abdominal markings, by the wider vertex of the head, and by its small subapical and shallow apical notches on the lateral lobes of the ninth tergites. From *A. alleni* it can be separated by the long white pile on the dorsum of the abdomen, by the wider vertex of the head, by the white pile on the terminalia and by not having the middle portion of the ninth sternite extending to apical third of ninth hemitergites, the middle portion does not extend beyond transverse portions of interbasal folds.

Apiocera alleni n. sp.

Male.—Large, robust. Mesonotal hair brown; abdominal hair beneath white; macrochaetae black throughout. Abdominal segments one through four predominantly black; terminalia piceous, pile black. Pteropleura with a conspicuous tuft of white hair in front of metathoracic spiracles. Dorso-caudal angle of mesopleura with tuft of white hair and three to four black macrochaetae. Compound eyes separated from lateral ocelli on vertex by less than the width of a lateral ocellus. *Head* with white pollen and pile on front; antennae black, grey pollinose, white pilose. *Mesonotum* white pollinose (rubbed), macrochaetae black. *Abdomen* with pile on dark areas black; black area on second segment interrupted at sides and along apical margin nearly to middle; third segment all black basally, narrowly interrupted laterally; fourth segment black except for narrow apical border; terminalia with median portion of ninth sternite slender, projecting posteriorly beyond visible transverse projections of interbasal folds (Plate 4, Fig. 6). *Legs* black, macrochaetae black; pulvilli about three-fourths length of claws. Length 23 mm., width 5 mm.

Female.—Unknown.

Holotype male in the author's collection, taken on the desert east of Victorville, San Bernardino County, California, June 27, 1932, by R. P. Allen after whom the author takes pleasure in naming the species. One male paratotype specimen in Mr. Allen's collection.

This species is most closely allied to *Apiocera aldrichi* Painter which it closely resembles in size, coloration and maculation. *Apiocera alleni* is, however, readily distinguished from this species by the absence of white pollen along the apical margin of the third abdominal segment, by the unemarginate inner apical margin of the lateral lobes of the ninth tergite and by the narrow shape and long length of the middle projection of the ninth sternite.

Apiocera parkeri n. sp.

Male.—Medium sized, narrow. Mesonotal hair long, brown, abdomen with hair on segments one to four yellowish-brown above, segments five to seven white; thoracic and leg macrochaetae predominantly black. Second abdominal segment with basal two-thirds black, apical third white, narrow, median, dorsal, black extension to apex of segment; segment three entirely black above; segment four with narrow, apical, white border; black bands on segments two and three interrupted laterally, piceous, white pollinose, pile black. Pteropleura with dispersed tuft of white hair in front of metathoracic spiracles. Dorso-caudal angle of mesopleura with three to four black macrochaetae. Compound eyes separated from lateral ocelli on vertex by little more than the width of a lateral ocellus. *Head* with front white pollinose and pilose; antennae black, white pollinose and pilose. *Mesonotum* with brown pollen, macrochaetae black. *Abdomen* white pollinose except in dark areas; segments five to seven white; terminalia with median portion of ninth sternite expanded, membranous, lateral lobes of ninth sternite without transverse median incision, transverse projections of interbasal folds narrowly protruding into ventral opening, projection irregular in shape (Plate 4, Fig. 1). *Legs* with femora black, tibiae and tarsi reddish-brown, macrochaetae mostly black; pulvilli about three-fourths length of claws. Length 17.5 mm., width 3.5 mm. (Plate 3, Fig. 4).

Female.—Similar to the male but with head yellow pollinose, thorax with both black and white macrochaetae, abdominal hairs white, abdomen with lateral, triangular black spots on segments two and three. Length 18.5 mm., width 4 mm.

Holotype male in the writer's collection, taken at Blythe, Riverside County, California, April 19, 1939 (F. H. Parker); allotype female also in the writer's collection taken at the type locality April 24, 1939, by F. H. Parker after whom the writer takes pleasure in naming the species. Thirty-one designated paratotypes distributed in the collections of R. H. Painter, F. H. Parker, T. G. Aitken and the author. Two paratypes from Ehrenberg, Yuma County, Azirona, April 16, 1939, (F. H. Parker) in the writer's collection.

This species is most closely allied to *Apiocera aldrichi* Painter and *Apiocera trimaculata* Painter. It can be distinguished from *A. aldrichi* by its smaller

size, by the black basal two-thirds of the second abdominal segment, by the completely black third abdominal segment, by the evenly rounded inner apical margin of the lateral lobes of the ninth tergite, and by the expanded membranous median portion of the ninth sternite. The terminalia of *A. parkeri* resemble closely those of *A. trimaculata* with which it appears to be most closely allied. It can be distinguished from this species by the presence of black macrochaetae on the dorso-caudal angle of the mesopleura, by the black color of most of the macrochaetae throughout, by the transverse black abdominal markings, by the

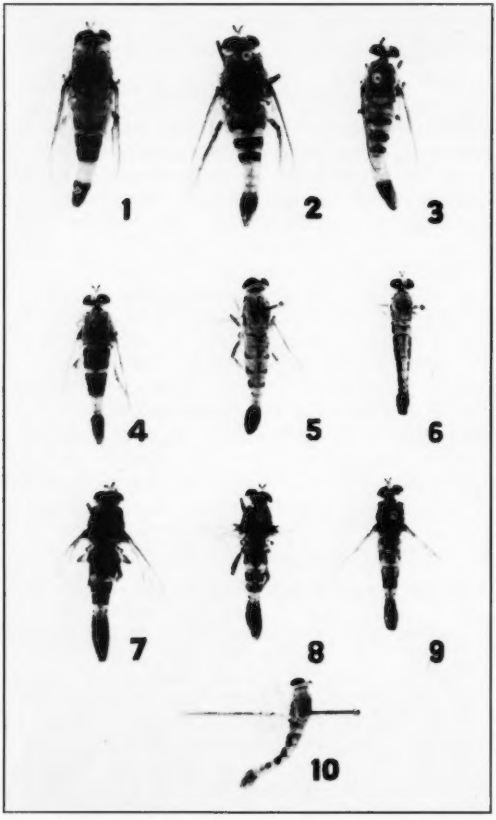


PLATE 3: Figs. 1-10. Males of *Apiocera* species. 1, *A. aldrichi* Painter. 2, *A. hispida* Cazier. 3, *A. pearcei* Cazier. 4, *A. parkeri* Cazier. 5, *A. augur* Osten Sacken. 6, *A. infinita* Cazier. 7, *A. haruspex* Osten Sacken. 8, *A. haruspex* Osten Sacken. 9, *A. haruspex* Osten Sacken. 10, *A. intonsa* Cazier.

black pilose terminalia and by having the median portion of the ninth sternite more prolonged posteriorly.

Apiocera exta n. sp.

Male.—Medium sized, narrow. Mesonotal hair brown, abdominal hair black on markings, white elsewhere; thoracic and leg macrochaetae black. Abdominal segments two, three and four predominantly black dorsally; terminalia piceous, pile black. Pteropleura with tuft of white hair in front of metathoracic spiracles. Dorso-caudal angle of mesopleura with four strong, black macrochaetae. Compound eyes separated from lateral ocelli on vertex by less than width of a lateral ocellus. *Head* with front white pollinose and pilose; antennae black, white pollinose and pilose. *Mesonotum* with brown pollen, macrochaetae black. *Abdomen* greyish pollinose; second and third segments with broad, median, dorsal, black bands, interrupted laterally; fourth segment with wide median band complete laterally; terminalia with median portion of ninth sternite expanded, membranous, lateral lobes of ninth sternite without transverse, median incision, transverse projection of interbasal folds not visible from beneath (Plate 4, Fig. 2). Legs with femora and tibiae black, tarsi reddish-brown; pulvilli about three-fourth length of claws. Length 17.5 mm., width 4 mm.

Female.—Unknown.

Holotype male in the writer's collection, taken in the Panamint Mountains, Inyo County, California, May 29, 1937 (L. R. Gillogly).

This species is most closely allied to *Apiocera aldrichi* Painter and *Apiocera caloris* Painter. It can be readily separated from *A. aldrichi* by its smaller size, by the evenly rounded inner edges of the lateral lobes of the ninth tergite, by the more membranous median portion of the ninth sternite and by having the transverse projections of the interbasal folds short and not protruding into ventral opening. From *A. caloris* it can be distinguished by its black macrochaetae, by its brown thoracic pile, by the black pile on the terminalia, by the piceous color of the terminalia and by having the transverse projections of the interbasal folds short and not protruding into ventral opening. *Apiocera exta* appears to be somewhat more closely allied to *A. caloris* because of their similar terminalia, abdominal patterns and size.

Apiocera clavator Painter

Apiocera clavator Painter, 1936, Bul. Univ. Kans., **37**:196-197.

Small, narrow; macrochaetae predominantly black, white on head, femora and coxae, pile white on white pollinose portions, black on mesonotum, abdominal dorsum, terminalia, tibiae and tarsi; abdomen with black, subquadrate lateral spots on segments two to seven, spots occasionally convex on upper margin, spot on fourth segment largest, spots diminishing in size posteriorly and less so anteriorly; terminalia piceous (Plate 4, Fig. 9). Length 16 mm.

Type locality: Colima, Mexico.

A small species resembling *A. bilineata* Painter and *A. interrupta* Painter

in the abdominal markings but easily separated from these species by its darker color and entirely different male terminalia.

Apiocera intonsa n. sp.

Male.—Medium sized, narrow. Mesonotal hair black, abdominal hair black above, white beneath; thoracic macrochaetae black, macrochaetae on legs white. Abdominal segments two through six with black lateral spots; terminalia reddish-brown, pile black. Pteropleura without tuft of white hair in front of metathoracic spiracles. Dorso caudal angle of mesopleura bare. Compound eyes separated from lateral ocelli by more than the width of a lateral ocellus on vertex. *Head* with white pollen and pile on front, six black macrochaetae on posterior surface; antennae with segments one and two yellowish, segment three black, pile throughout white. *Mesonotum* brown pollinose, macrochaetae black. *Abdomen* brownish pollinose above, white beneath; segments two, three, four and five with large black lateral spots, ventral margin of spots straight, dorsal margin obtusely rounded, segment six with irregular light-brown lateral spot; terminalia with limits of basistyle and disistyle of ninth sternite marked with deep, rather wide transverse incision on inner margn, median portion of ninth sternite with lateral tufts of white-tipped black hair, dististyles with subapical flare of long, white-tipped, black hair extending well beyond apices, not compact (Plate 4, Fig. 15). *Legs* uniformly reddish-brown; pulvilli about three-fourths length of claws. Length 16 mm., width 3 mm. (Plate 3, Fig. 10).

Female.—Unknown.

Holotype male in the writer's collection, taken at San Carlos, Gila County, Arizona, September 3, 1938 (F. H. Parker). One male paratype from 23 miles south of Vidal, Riverside County, California, June 12, 1940 (R. G. Dahl) in Mr. Dahl's collection.

This species is most cosely allied to *Apiocera interrupta* Painter and *Apiocera bilineata* Painter being, perhaps, more nearly related to the former. It can, however, be distinguished from *A. interrupta* by the black pile on the mesonotum and terminalia, by the black thoracic macrochaetae, and by the subapical flare of long, white-tipped, black hair on the dististyles of the terminalia. The last mentioned character is, as far as known, evident in only one other species, that is, the South African *Apiocera braunsi* Melander. Judging from the illustration given by Melander the terminal hairs in *A. braunsi* are longer and more closely placed than in *A. intonsa*. *Apiocera intonsa* can be distinguished from *A .bilineata* by the black thoracic macrochaetae, by the black pile on the terminalia, by the wider incision separating the basistyles and dististyles, by having the upper edge of the abdominal black spots convex, by having the pulvilli three-fourths as long as the claws and by the subapical flare of long, white-tipped, black hair on the dististyles.

Apiocera interrupta Painter

Apiocera interrupta Painter, 1936, Bul. Univ. Kans., **37**:192-193.

Rather large, robust; macrochaetae predominantly white throughout; abdo-

men with lateral rows of spots on segments two to seven, spots straight on lower margin, convex on upper margin; terminalia reddish-brown, pile white except for a little blackish or brownish pile on the undersurface; pulvilli about three-fourths the length of the claws. (Terminalia, Plate 4, Fig. 13). Length 19 mm.

Type locality: Los Angeles, California (Male). Additional specimens recorded from San Diego County, California; Indo, Riverside County, California, August 5, 1935.

This species is most closely allied to *A. bilineata* Painter and *A. melanura* Cazier. From *A. bilineata* it can be distinguished by having the abdominal spots convex above and by having the pulvilli usually more than half as long as the claws. It can be separated from *A. melanura* by being white pollinose, by the white macrochaetae of the thorax, by the white pile on the terminalia and abdomen and by having the terminalia pale brown in color.

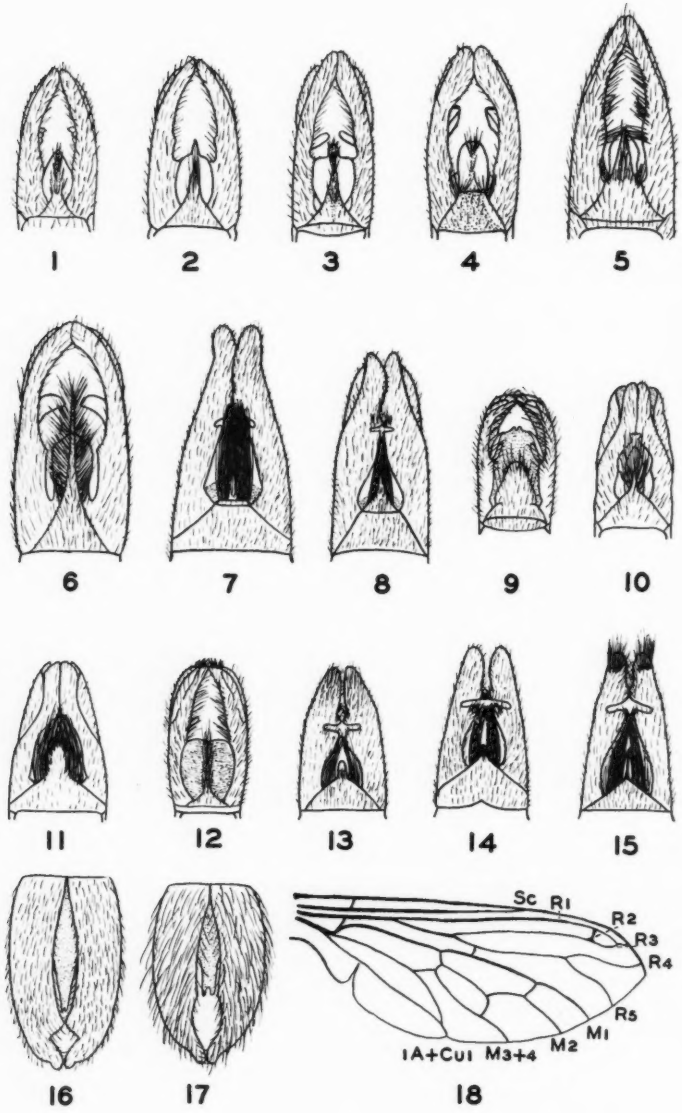
Apiocera melanura n. sp.

Male.—Medium sized, narrow. Mesonotal hair brown, abdominal hair brown above, white beneath; thoracic macrochaetae black, macrochaetae on femora and tibiae white. Abdominal segments two through five with lateral black markings, rather widely interrupted between segments; terminalia piceous, pile black, Pteropleura without tuft of white hair in front of metathoracic spiracles. Dorso-caudal angle of mesopleura bare. Compound eyes separated from lateral ocelli on vertex by more than width of a lateral ocellus. *Head* with brownish pollen on vertex; front white pollinose and pilose; antennae with segments one and two yellowish, pile white, third segment dark. *Mesonotum* with brown and grey pollen irregularly intermixed; thoracic macrochaetae predominantly black. *Abdomen* brownish pollinose above, white beneath; lateral elongate markings with lower margin straight, upper margin obtusely convex; terminalia with rather deep, narrow incision separating the dististyles from the basistyles (Plate 4, Fig. 14). *Legs* predominantly yellow, occasionally mixed with black; pulvilli a little more than one-half length of tarsal claws. Length 18 mm., width 3 mm.

Female.—Unknown.

Holotype male in the collection of the United States National Museum, taken in Gila Valley, Gila County, Arizona, July 29, 1933 (F. H. Parker).

This species is most closely allied to *Apiocera interrupta* Painter with which it agrees in the character of the abdominal markings. It can, however, be distinguished from *A. interrupta* by its brownish pollinose appearance, by the black macrochaetae on the thorax, by the black abdominal and terminalia pile and by the piceous color of the terminalia. *Apiocera melanura* can be separated from *A. intonsa* Cazier, which is also in this group, by having all macrochaetae on the posterior surface of the head white, by the narrow abdominal markings, by the shorter pulvilli, by not having the subapical flare of long, white-tipped black hair on the dististyles and by having the terminalia piceous. From *A. infinita* Cazier it can be distinguished by its interrupted lateral abdominal markings and by having the upper margin of these markings convex.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Apiocera bilineata Painter

Apiocera bilineata Painter, 1932, Ann. Ent. Soc. Amer., **25**:351-352; Painter, 1936, Bul. Univ. Kans., **37**:191.

Medium sized, narrow; macrochaetae predominantly white throughout; abdomen with narrow, black, lateral band, formed by subquadrate spots on each segment from two to five, irregular spot on six; terminalia reddish-brown, clothed with black pile at base, white pile apically; pulvilli about half as long as the claws. (Terminalia, Plate 4, Fig. 13). Length 15-17 mm.

Type locality: White Sands, Otero County, New Mexico, August 8, 1931 (Male). One additional specimen recorded by Painter (1936) from Cameron County, Texas.

This species is allied to the two preceding species but is probably more closely related to *A. infinita* Cazier. It can be separated from this species by its pale brown terminalia and by the short pulvilli.

Apiocera infinita n. sp.

Male.—Medium sized, narrow. Mesonotal hair black; abdominal hair black above, white beneath; thoracic macrochaetae black, macrochaetae on femora and tibiae white. Abdominal segments two through seven with oblong, black, lateral markings, scarcely interrupted between segments, terminalia piceous, pile black. Pteropleura without tuft of white hair in front of metathoracic spiracles. Dorso-caudal angle of mesopleura bare. Compound eyes separated from lateral ocelli on vertex by more than width of a lateral ocellus. *Head* with white pile and pollen on front; antennae yellowish, pile white. *Mesonotum* brown pollinose, thoracic macrochaetae pale to black. *Abdomen* brownish pollinose above, white beneath; lateral markings with both lower and upper margins nearly straight; terminalia with rather deep, narrow incision separating the dististyles from the basistyles (Plate 4, Fig. 14). *Legs* with femora black except for apex, tibiae and tarsi reddish-brown; pulvilli about three-fourths length of claws. Length 16 mm., width 3 mm. (Plate 3, Fig. 6).

Female.—Unknown.

Holotype male in the writer's collection, taken at Blythe, Riverside County, California, September 16, 1938 (F. H. Parker). Eight paratopotypical speci-

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PLATE 4: Figs. 1-15. Terminalia venter of *Apiocera* species. 1, *A. trimaculata* Painter and *A. parkeri* Cazier (illustrated). 2, *A. exta* Cazier. 3, *A. caloris* Painter and *A. pearcei* Cazier. 4, *A. beameri* Painter. 5, *A. aldrichi* Painter. 9, *A. alleni* Cazier. 7, *A. haruspex* Osten Sacken. 8, *A. martinorum* Painter. 9, *A. clavator* Painter. 10, *A. convergens* Painter. 11, *A. notata* Painter. 12, *A. augur* Osten Sacken. 13, *A. bilineata* Painter and *A. interrupta* Painter. 14, *A. infinita* Cazier and *A. melanura* Cazier. 15, *A. intonsa* Cazier.

Figs. 16-17. Terminalia tergites of *Apiocera species*. 16, *A. aldrichi* Painter. 17, *A. hispida* Cazier.

Fig. 18. Wing of *Laphria sicula* McAtee *(Asilidae)*.

mens distributed in the collections of R. H. Painter, F. H. Parker, T. G. Aitken and the author.

This species is most closely allied to *Apiocera bilineata* Painter but can at once be separated by its pale to black thoracic macrochaetae, by its piceous terminalia, by the black pile on the terminalia and by having the pulvilli three-fourths as long as the tarsal claws.

Apiocera haruspex Osten Sacken

Apiocera haruspex O. S., 1877, Bul. U. S. Geol. and Geog. Survey of the Territories, **3**:283-284; Painter, 1932, Ann. Ent. Soc. Amer., **25**:352-353; Painter, 1936, Bul. Univ. Kans., **37**:191-192.

Medium sized, rather narrow; macrochaetae black throughout; abdominal markings variable, first segment brown pollinose except for elongate lateral white spots, second segment brown basally, median black triangular spot with apex nearly reaching posterior margin, two unconnected lateral oblong black spots, remainder white, third segment with black median triangular extension from apical half extending to base, bisecting white basal band, third segment same as second, fifth and sixth white except for brown lateral and median spots, seventh and eighth brown except for lateral angles; terminalia piceous, pile black (Plate 4, Fig. 7). Length 17-20 mm.

Type locality: Yosemite Valley, Mariposa County, California. Widespread throughout California and extending into Idaho, Washington, Wyoming, British Columbia, Oregon and Arizona.

The markings in this species are extremely variable (Plate 3, Figs. 7, 8, and 9) and are of little aid in separating the species from its allies and are difficult to use. It is closely allied to *A. notata* Painter from which it can be separated by having the ninth tergite notched at the apex and by having the terminalia piceous rather than black. From *A. martinorum* Painter it can be separated by its broadly blackened third and fourth abdominal segments, and by minor variations in other abdominal markings.

Apiocera notata Painter

Apiocera notata Painter, 1936, Bul. Univ. Kans., **37**:199-200.

Large, moderately robust; macrochaetae of head and four front coxae mostly white, remainder black; abdomen with first segment brown pollinose, darker in center, second segment brown pollinose on anterior margin, white on posterior margin, separated by three connected black triangles, third segment with two brown spots along anterior margin, remainder black, fourth segment black with two small white spots on anterior margin, fifth and sixth segments white pollinose, seventh mostly brown pollinose on the dorsum; terminalia piceous, pile black (Plate 4, Fig. 11). Length 20 mm.

Type locality: Campo, San Diego County, California, August 10, 1935.

Closely allied to *A. haruspex* O. S. but readily separated by its black terminalia and by lacking the notch on the lateral lobes of the ninth tergite.

Apiocera martinorum Painter

Apiocera martinorum Painter, 1936, Bul. Univ. Kans., **37**:197-198.

Medium sized, rather slender; macrochaetae predominantly black, pile white except for the short hairs on the metanotum, terminalia and the black spots on the abdomen which are black; abdomen with first segment brownish with two white spots laterally, second segment brownish at base, to which four blackish spots are more or less connected, remainder of segment white, third segment with four spots separated by white pollen, fourth segment with inner lateral spots broader at apex and almost united with the others on this margin, last three segments white pollinose, with a central brown dorsal spot; terminalia brown, pile black (Plate 4, Fig. 8). Length 19 mm.

Type locality: Adrian, Malheur County, Oregon, July 22, 1932 (Owyhee River sand dunes). Additional localities include: Roswell Bench, Parma, Canyon County, Idaho.

This species is allied to both *A. haruspex* O. S. and *A. convergens* Painter but can be separated from both by the male terminalia.

Apiocera convergens Painter

Apiocera convergens Painter, 1936, Bul. Univ. Kans., **37**:196.

Medium sized, rather slender; macrochaetae black; pile white except for short black hair on thoracic and abdominal dorsum and on the terminalia; abdomen with a central black triangle with its base on segment two, apex on segment five, base of each segment brownish, apex black, interrupted at extreme apices of segments two and four by narrow white band, central black triangle separated from two rows of black lateral subquadrate spots by a white stripe on each side; terminalia piceous, pile black (Plate 4, Fig. 10). Length 18 mm.

Type locality: California.

Although allied to *A. martinorum* Painter it can be separated by not having a notch at apex of lateral lobes of ninth tergite, and by the abdominal markings. It can be separated from *A. haruspex* O. S. by the presence of black spots on abdominal segments three and four. In *A. haruspex* these segments are broadly black.

Apiocera augur Osten Sacken

Apiocera augur O. S., 1887, Biologia Centrali Americana, Diptera, **1**:212-213; Painter, 1932, Ann. Ent. Soc. Amer., **25**:354-355; Painter, 1936, Bul. Univ. Kans., **37**:192.

Medium sized, rather narrow; macrochaetae predominantly black; abdominal segments two, three and four with lateral triangular, brown maculations, segment five with small lateral spot; terminalia piceous, pile brown (Plate 4, Fig. 12). Length 16-18 mm. (Plate 3, Fig. 5).

Type locality: Presidio, Mexico. Additional records include numerous localities in Texas and several in New Mexico.

The species here described as *A. augur* has receitly been suspected as not being that species by Painter, in litt., and may possibly represent a new species.

Genus RHAPHIOMIDAS Osten Sacken

Rhaphiomidas Osten Sacken, 1877, Bul. U. S. Geol. and Geog. Survey of the Territories, **3**:281; Osten Sacken, 1878, Wash. Smith. Misc. Coll. p. 85; Osten Sacken, 1883, Berliner Ent. Zeit., **27**:293; Coquillett, 1891, West Amer. Sci., (56) **7**:84-86; Williston, 1893, Kansas Univ. Quart., (3) **1**:101-118; Towsend, 1895, Proc. Cal. Acad. Sci., (2) **4**:601-607; Towsend, 1901, Trans. Amer. Ent. Soc., **27**:163-164; Williston, 1908, Manual of N. A. Diptera, p. 188-189; Hermann, 1909, Deutsch. Ent. Zeitschr. Beiheft, **1909**:104-122; Coquillett, 1910, Proc. U. S. Nat. Mus., **37**:600; Norris, 1936, Jour. Royal Soc. of West. Australia, **22**:64; Painter, 1936, Bul. Univ. Kans., **37**:188.

Apomidas Coquillett, 1892, Canad. Ent., **24**:314-315 (Type *A. trochilus* Coq.; type locality, Merced County, California); Norris, 1936, Jour. Royal Soc. of West Australia, **22**:50; Painter, 1936, Bul. Univ. Kans., **37**:188. *(New synonym).*

Large robust, setigerous, thinly to densely pilose flies. *Head* large, eyes dichoptic in both sexes, vertex convex, with three ocelli; antennae three-segmented; palpi one-segmented; mouthparts elongate, labella not greatly enlarged. *Thorax* well developed, side and hind margins setose, metathorax with a large conical swelling on lateral lobe of postnotum; scutellum large, setose. *Wings* (Plate 1, Fig. 5) with R4, R5, M1 and M2 terminating on anterior margin, discal cell always present. *Abdomen* gradually tapering apically; legs long and slender, not fitted for grasping, empodia lacking. *Terminalia* large, simple; lateral lobes of ninth tergite large, enclosing the genital and anal organs, ninth sternite and gonostyles forming ventral surface; gonostyles closely united to ninth sternite basally, not articulate and not differentiated into basistyle and dististyle; interbasal folds small, represented by a short, rounded projection on inner surface of basistyle; parameres without projections, consisting of two rounded sclerites lying laterally to penis valves, and dorsal and anterior to base of interbasal fold; penis valves forming a basal-ventral support for the penis which is thick at base, abruptly constricted into cylindrical up-curved projection apically; proctiger dorsal, membranous and trilobed apically; inner surface of lateral lobes of ninth tergite concave or convex, generally without differentiated area but occasionally with a series of sharp carinae along margin at right angles to edge.

Genotype: *Rhaphiomidas episcopus* Osten Sacken.

Type locality: Lower California, Mexico.

The genus *Apomidas* is regarded as a synonym only after a careful study was made of the unique female type in the United States National Museum. The only character separating this genus from *Rhaphiomidas* is the open anal cell in the wing. At the time Coquillett (1892) described the genus variations in the wing veins of *Apiocera* were unknown and no wing variations had been observed in *Rhaphiomidas*, thus perhaps justifying its description. However, much variation is now known in the wings of *Apiocera* and Painter (1936) recorded a specimen of *Rhaphiomidas acton* Coq. which had the anal cell narrowly open. In the specimens before the writer there is considerable variation in the position at which 1A unites with Cu1 so as to close this cell. Often Cu1 unites with 1A a considerable distance from the wing margin, or they may not be united except by a thickening of the wing margin. In the latter case the anal cell

appears to be narrowly open. Also the discovery of many additional specimens of the species, all having the anal cell closed or only narrowly open, shows that the type of *Apomidas* is undoubtedly nothing more than a wing variant of *Rhaphiomidas*. The type species *Apomidas trochilus* Coq. is distinct and is therefore retained.

Rhaphiomidas can be readily distinguished from *Apiocera* by its large size, relatively simple terminalia, one-segmented palpi, wing venation and by the large conical swellings on the lateral lobes of the postnotum. The latter character apparently finds an intermediate form in *Neorhaphiomidas pinguis* Norris (1936) but in the Nearctic region no intermediates are known.

Specific differentiation in this genus is much more difficult than in Apiocera since the terminalia are useful, for the most part, only in defining groups. *Rhaphiomidas episcopus* O. S., *R. xanthos* Towns., *R. painteri* Cazier, *R. trochilus* (Coq.), *R. aitkeni* Cazier, *R. abdominalis* Cazier and *R. terminatus* Cazier represent one group in which the terminalia are narrow (Plate 2, Figs. 5-10). *Rhaphiomidas maculatus* Cazier, *R. acton* Coq. and *R. maehleri* Cazier have the terminalia large and robust (Plate 2, Figs. 1-4). *Rhaphiomidas parkeri* Cazier is, at present, the only species in a third grouping that is more distinct in this character than either of the above groups. In the latter species the terminalia are nearly cylindrical and the inner surfaces of the lateral lobes of the ninth tergites are convex rather than concave (Plate 2, Fig. 11).

Key to the Species of Rhaphiomidas

MALES

1. Abdomen unicolorous dark brown or black. ..... *episcopus* Osten Sacken
   Abdomen not unicolorous brown or black. 2
2. Macrochaetae of hind tibiae wholly or in greater part dark brown or black. 3
   Macrochaetae of hind tibiae not brown or black. 6
3. Lateral lobes of ninth tergite bicolored, median portion black or dark brown, margins orange. ..... *trochilus* Coquillett
   Lateral lobes of ninth tergite unicolorous orange, not with above combination. 4
4. Abdomen black or dark brown, each segment with posterior marginal band of yellow; scutellar and posterior mesonotal setae brown or black. ..... *terminatus* Cazier
   Abdomen orange, or with dark markings on segments three to six confined to mid dorsum; scutellar and posterior mesonotal setae yellow or orange. 5
5. Compound eyes separated from lateral ocelli by the width or more than width of a lateral ocellus; abdominal segments three to six with dark areas on mid-dorsum. ..... *abdominalis* Cazier
   Compound eyes separated from lateral ocelli by less than one-half width of a lateral ocellus; abdominal segments three to six unicolorous orange, without dark mid-dorsal areas. ..... *xanthos* Townsend
6. (2) Gonostyles extending from apical fourth to apex of lateral lobes of ninth tergite; terminalia comparatively small. 7
   Gonostyles extending little more than one-half distance to apex of lateral lobes of ninth tergite; terminalia large, robust. 9
7. Vertex with each compound eye separated from lateral ocelli by about one-half the width of a lateral ocellus; terminal antennal segment short, robust, ventral sensory area of third segment confined to apical third; abdominal segments bordered posteriorly with brown or black. ..... *painteri* Cazier

Vertex with each compound eye separated from lateral ocelli by the width or more than width of a lateral ocellus; terminal antennal segment elongate, ventral sensory area of third segment extending from basal fourth to near apex; abdominal segments bordered posteriorly with yellow. 8

8. Gonostyles extending to or beyond apex of lateral lobes of ninth tergite; lateral lobes of ninth tergite black, narrowly margined with orange; ninth sternite black. .....*parkeri* Cazier

Gonostyles extending to apical fourth of lateral lobes of ninth tergite; lateral lobes of ninth tergite unicolorous orange; ninth sternite orange. .....*aitkeni* Cazier

9. (6) Abdominal mid-dorsal black markings large, often extending to posterior margin on one or more segments from one to six; macrochaetae of hind trochanters for the most part black. .....*maculatus* Cazier

Abdominal mid-dorsal markings lacking or represented by isolated spots; macrochaetae of hind trochanters for the most part yellow. .....
.....*maehleri* Cazier and *acton* Coquillett

FEMALES

1. Abdomen unicolorous dark brown or black. .....*episcopus* Osten Sacken

Abdomen not unicolorous dark brown or black. 2

2. Macrochaetae of hind tibiae wholly or in greater part dark brown or black. 3

Macrochaetae of hind tibiae yellow. 4

3. Vertex highest behind the lateral ocelli; narrow between the eyes; medium sized. .....*xanthos* Townsend

Vertex highest between the lateral ocelli; wide between the eyes; size large. .....
.....*trochilus* Coquillett and *terminatus* Cazier

4. (2) Abdominal markings in the form of transverse bands, if broken laterally the middle spots become progressively larger toward the base of the abdomen. 5

Abdominal markings forming only mid-dorsal spots which become larger toward the apex of the abdomen. .....*maculatus* Cazier and *acton* Coquillett

5. Abdominal segments two to four yellow with narrow, brown or black posterior margins. .....*painteri* Cazier

Abdominal segments two to four black with broad, yellow posterior margins. 6

6. Retrorse abdominal pile beginning on the fourth segment; first abdominal segment without yellow maculations. .....*parkeri* Cazier

Retrorse abdominal pile beginning on the fifth segment; first abdominal segment with yellow maculations. .....*maehleri* Cazier

The females of *Rhaphiomidas abdominalis* Cazier and *R. aitkeni* Cazier are unknown at present.

Rhaphiomidas episcopus O. S.

Rhaphiomidas episcopus O. S., 1877, Bul. U. S. Geol. and Geog. Survey of the Terr., **3**:281 (female); Coquillett, 1891, West Amer. Sci., (56)**7**:85; Townsend, 1895, Proc. Cal. Acad. Sci., (2) **4**:603 (male); Painter, 1936, Bul. Univ. Kans., **37**:188.

Female.—Black, sparsely clothed with yellow pile and black macrochaetae. *Head* with front rather sparsely clothed with yellow pie; vertex with three ocelli, compound eyes separated from lateral ocelli by little more than the width of a lateral ocellus; antennae brown, terminal segment orange beneath, sensory area large, macrochaetae on first and second segments brown and yellow mixed; mouth parts slightly longer than one-half body length; beard white. *Thorax* black, grey pruinose, sparsely clothed with yellow pile, lateral macrochaetae brown. *Abdomen* black, glabrous medially, sides and apical sub-

margins of segments one to three sparsely clothed with yellowish pile, fourth segment with black pile dorsally. *Undersurface* dark except for anterior tibiae and tarsi and middle tarsi which are yellow, macrochaetae of legs dark in color. Length 20 mm., width 6 mm. (Plate 2, Fig. 10).

Type locality: California (probably Lower California, Mexico). Additional localities include El Taste, Lower California, September, 1893 (Eisen).

Judging from the description of the male, as given by Townsend (1895), it agrees with the female in most respects. The terminalia are apparently small, as they are in *R. xanthos* Townsend, and are clothed at the base with black pile. The species can be readily distinguished from all others by its uniform black color.

Rhaphiomidas xanthos Townsend

Rhaphiomidas xanthos Towns., 1895, Proc. Cal. Acad. Sci., (2) **4**:606 (male); Painter, 1936, Bul. Univ. Kans., **37**:189.

Rhaphiomidas mellifex Towns., 1895, Proc. Cal. Acad. Sci., (2) **4**:604 (female); Coquillett, 1891, West Amer. Sci., **7**:85 *(episcopus)*; Painter, 1936, Bul. Univ. Kans., **37**:189. *(New synonym).*

Male.—Comparatively small; abdomen and terminalia yellow, thorax black, grey pollinose. *Head* with the front rather densely clothed with yellowish pile; vertex narrow, inner margins of compound eyes separated from lateral ocelli by less than half the width of a lateral ocellus; antennae orange, macrochaetae yellow, third segment little longer than one and two combined, rounded at middle; mouthparts about one-half length of body. *Thorax* clothed with yellowish pile, macrochaetae yellow and brown. *Abdomen* with first and second segments dark medially, remainder yellow; clothed with yellow pile: terminalia with lateral lobes of ninth tergite short and narrow, gonostyles extending to apical fourth of lateral lobes. *Legs* yellow, macrochaetae black or brown, front femora slightly darker than others. Length 17.5 mm., width 5 mm. (Plate 2, Fig. 8).

Female.—Medium sized; abdomen bicolored. *Head* as in male except that inner margins of compound eyes are separated from lateral ocelli by about the width of an ocellus. *Thorax* as in the male. *Abdomen* with basal two-thirds of segments two, three and four brown, first segment with narrow apical yellow band; segments rather sparsely clothed with white pile. *Legs* as in male except that femora are more brownish. Length 24 mm., width 7 mm.

Lectotype male in the collection of the University of Kansas, selected from two male specimens labeled "type" by Townsend and collected at El Taste, Lower California, Mexico, September (Eisen). *Rhaphiomidas xanthos* was selected to represent this species because of its sex, the male having the added advantage of certain characters not available in the female. A female from El Taste, Lower California, September, in the collection of the University of Kansas labeled *Rhaphiomidas mellifex* Towns. "type" is here designated as lectotype of this species (synonym).

Two additional topotypical males and one topotypical female labeled "type" *(R. mellifex)* are in the same collection as the lectotypes. The type of

this species was supposedly destroyed in the San Francisco fire of 1906 (Painter, 1936). However, additional information indicates that all type specimens in the California Academy collection were carried to safety and the reason this type was not included in the list given by E. C. Van Dyke (1906)[11] is that there were no Diptera types in the collection at that time. The specimens designated above are perhaps Townsend's original types. There is some doubt as to Townsend's published type locality, San Jose del Cabo, as all specimens are labeled El Taste.

Rhaphiomidas mellifex Townsend is relegated to synonymy not only because of its morphological similarities but also because of the lack of evidence for its specific status. Both species, *R. mellifex* and *R. xanthos,* were collected at the same place and time by Eeisen; the former species was represented by six females and the latter by eleven males. The opposite sexes of both species remained undiscovered. Those referred to by Townsend (1901, 1895) are described as new in this paper *(R. painteri* and *R. terminatus)* and are rather remotely related to *R. xanthos* and *R. mellifex.* Furthermore, since it is now known that there are other sexually dichromatic species in the genus it does not seem unreasonable to conclude that *R. mellifex* is merely the female of *R. xanthos.* Townsend (1895, p. 605) states as follows: "Although my six specimens [*R. mellifex*] are all females, and my eleven specimens of *xanthos* are all males, and moreover both were largely collected at the same time and place, still I do not believe that I am describing two sexes of the same species. The sexes of *Rhaphiomidas* appear to closely agree in coloration. Coquillett assures us that the sexes of *action* are alike in coloring." Townsend's reason for describing *R. xanthos* is obviously based on the incorrect assumption given by Coquillett.

Rhaphiomidas trochilus (Coq.)

Rhaphiomidas trochilus (Coq.), 1892, Canad. Ent., **24**:315, female, *(Apomidas);* Norris, 1936, Jour. Roy. Soc. of West. Australia. **22**:50; Painter, 1936, Bul. Univ. Kans., **37**:188.

Male.—Large, robust; head, thorax, abdomen and terminalia clothed with long grey pile; thorax black, grey pollinose; abdominal segments black with narrow, yellow apical borders; lateral lobes of ninth tergite black bordered with orange. *Head* slightly wider than anterior angles of thorax, posterior surface and front densely clothed with grey pile, vertex and sides of face rather sparsely pilose; ocelli convex, brown, anterior ocellus same size as posterior ones; antennal segments one and two clothed with long grey pile, first segment dark brown, second yellowish-orange, third segment glabrous, orange; palpi grey, apically with grey pile; mouthparts less than half the length of the body. *Thorax* black, grey pollinose, sides of disk with wide dark area, narrowly, obliquely broken at basal third, middle of disk with two rather wide, parallel, proximate bands extending from apex to basal third, surface sparsely clothed with short grey pile, posterior margins of mesothorax and scutellum with long

11 Van Dyke, E. C., 1906, Ent. News, **17**:222.

grey macrochaetae; wings hyaline, anal cell closed (occasionally narrowly open). *Abdomen* gradually tapering to the narrow terminalia, rather sparsely clothed with grey pile; all segments black with grey pollen, posterior margin of each segment with narrow yellow band; terminalia narrow, black, narrowly bordered with orange, surface clothed with long grey pile, length 5 mm., width 3.5 mm. *Undersurface* grey pollinose, clothed with long grey pile, especially dense on coxae, abdominal sternites black with narrow lateral and apical borders; ninth sternite black with grey pile, gonostyles orange, arcuate; front and hind femora dark brown basally on sides and above, apical one-third orange-yellow, middle femora with upper surface dark brown on basal two-thirds, tibiae and tarsi orange-yellow, macrochaetae black or brown, pile grey, venter of basitarsi with short, stout, black spines. Length 30 mm., width 7 mm. (Plate 2, Fig. 7).

Female.—Similar to the male except for the usual sexual differences, larger size and more robust shape. Length 33 mm., width 8.5 mm.

Holotype female in the collection of the United States National Museum.

Type locality: Merced County, California. The thirty-one specimens examined were collected at Antioch, Contra Costa County, July, August and September; Ceres, Stanislaus County, August; Lindsay, Tulare County, August; and San Jacinto Mountains, Riverside County, July.

The type specimen of this species is a large female that has the anal cell widely open in both wings. In a few of the specimens listed above the anal cell is narrowly open in one wing and closed in the other. Otherwise the wings retain the generic characteristics of *Rhaphiomidas*. Other than this wing variation the species appears to be one of the most consistent in the genus as regards color and pigmentation. It is also the largest species, some of the females attaining 35 mm. in length.

The Antioch specimens were collected three or four miles east of Antioch in the barren sand hills along the south side of the San Joaquin-Sacramento River. The adults are exceedingly fast in flight and, unlike many asilids, do not habitually return to the same resting point after being disturbed. During flight the wings make a humming noise that is distinctly audible for a distance of twenty to thirty yards. None of the numerous specimens collected at this locality has been taken on or in association with flowers. Most of the specimens are found resting on the sand with the wings folded over the back or often extended at right angles to the body, the tips nearly touching the sand. Many specimens collected by T. Aitken and the writer on August 24, 1938, were taken in a barren, sandy depression in which were nests of various species of Bembicidae and Cerceridae *(Cerceris)*. The *Rhaphiomidas*, however, seemed in no way interested in the bembicids or cercerids or in their nests and were never observed carrying anything. They were not confined to this area and in other places nearby were without this association. Neither oviposition, copulation nor the immature stages were observed.

Rhaphiomidas terminatus n. sp.

Coquillett, 1891, West Amer. Sci., **7**:85 *(episcopus* O. S.); Townsend, 1895, Proc. Calif. Acad. Sci., (2) **4**:603-604 (*mellifex* Towns.).

Male.—Large, robust; abdominal segments black with narrow, yellow apical borders; lateral lobes of ninth tergite unicolorous orange. *Head* with eyes widely separated at vertex, front rather densely clothed with long grey pile; antennae with setigerous basal two segments brown, terminal segment orange, widened medially; mouthparts longer than one-half length of body, narrow. *Thorax* sculptured with pollen as in *trochilus;* macrochaetae white laterally, basally black or brown. *Abdomen* sparsely clothed with grey pile; segments yellow for apical third or less; terminalia small, narrow, unicolorous orange. *Legs* uniform brown, macrochaetae brown or black. Length 25.5 mm., width 6 mm.

Female.—Similar to the male except for the usual sexual differences. Length 25 mm., width 7 mm.

Holotype male, allotype female in the collection of the United States National Museum, collected at Los Angeles, California, by D. W. Coquillett.

This species is most closely allied to *Rhaphiomidas trochilus* (Coq.) from which it can be easily distinguished by its smaller size, longer mouthparts, smaller and uniformly orange terminalia. *Rhaphiomidas terminatus* has been confused with *R. episcopus* O. S. but differs in the bicolored abdomen and the widely separated compound eyes on the vertex.

Coquillett (1891) referred to these same two specimens as *R. episcopus*, obviously overlooking the fact that the latter species is smaller and has the abdomen uniformly black. Townsend (1895) pointed out that Coquillett was in error and that the species mentioned was new and that he was therein describing it as *R. mellifex*. However, in the description of *R. mellifex* no mention of the specimens recorded by Coquillett from Los Angeles County is made, the type locality being San Jose del Cabo, Lower California, Mexico. It has been shown that *R. mellifex* is the female of the sexually dichromatic *R. xanthos* and it is therefore impossible to refer the sexually monochromatic *R. terminatus* to this species. The latter species is much more closely related to *R. trochilus* on the basis of the terminalia and width of the vertex between the compound eyes.

Rhaphiomidas painteri n. sp.

Townsend, 1901, Trans. Amer. Ent. Soc., **27**:163 *(R. xanthos);* Painter, 1936, Bul. Univ. Kans., **37**:189 *(R. xanthos).*

Male.—Comparatively small; head and thorax predominantly black; abdomen with first segment and middle of second black, segments two to five orange except for narrow apical border. *Head* with inner margins of compound eyes separated from lateral ocelli by about one-half the width of an ocellus, front moderately densely clothed with white pile; antennae with segments one and two brown, clothed with long yellowish pile, terminal segment as long as one and two combined, orange, widest at middle; mouthparts slightly

longer than one-half the length of the body. *Thorax* black with two irregular, dull, orange spots laterally above wing insertions, grey pollinose, pile and macrochaetae yellowish; scutellum black, bordered apically with narrow orange band. *Abdomen* with dense yellowish pile throughout; segments two to four bordered apically with narrow, dark, transverse bands, each band about one-fourth width of segment, fifth segment obscurely banded; terminalia with lateral lobes of ninth tergite small, robust, strongly constricted subapically, ventral margin straight, gonostyles projecting posteriorly for about three-fourths length of lateral lobes of ninth tergite. *Undersurface* moderately densely clothed with yellowish pile; femora darkened proximally, tibiae and tarsi yellow. Length 20 mm., width 5.5 mm. (Plate 2, Fig. 9).

Female.—Same as male but with the pile more intact, that of thorax uniformly yellowish, dense, of first abdominal segment semi-erect, white, second, third and fourth segments with yellow recumbent, dense pile. Length 20 mm., width 5.6 mm.

Holotype male in the collection of R. H. Painter, taken at State College, New Mexico, September 23 (W. J. Baerg); allotype female in the United States National Museum Collection, taken at Las Cruces, New Mexico, September 10 (Townsend). The allotype specimen was collected dead on a side walk. A third topotypical female specimen of the species is in the collection of R. H. Painter but is in poor condition and appears to have been unhardened when killed. It differs from the allotype by its larger size, more robust shape, and by its more lightly colored femora.

Apparently most closely allied to *Rhaphiomidas xanthos* Towns. from which it can be at once separated by the wider vertex of the head, the yellow macrochaetae of the hind tibiae, the robust terminalia and by the apical dark bands on abdominal segments two to four. Due to the obscurity concerning the identity of *R. xanthos* this species was referred to by both Townsend and Painter as that species. It is not surprising to find that the New Mexican *R. painteri* is distinct from *R. xanthos* since over one-thousand miles separate their respective localities.

Raphiomidas aitkeni n. sp.

Male.—Relatively small, narrow; thorax moderately clothed with grey pile; abdomen yellow, median lunate markings black; lateral lobes of ninth tergite orange. *Head* slightly wider than anterior angles of thorax, vertex and front densely clothed with grey pile; ocelli white, concave, compound eyes separated from lateral ocelli by at least the width of an ocellus; antennal segments one and two black with grey pile, third segment glabrous, orange; palpi grey, pilose. *Thorax* black, yellow pollen marginal and in two parallel, longitudinal, discal bands, separated by more than their own widths, surface rather densely clothed with grey pile, posterior lateral margins of mesothorax and scutellum with long grey macrochaetae. *Abdomen* narrow, gradually tapering to terminalia, moderately clothed with grey pile; first segment black except for narrow apical margin, widest laterally, second segment about half and half black and yellow,

base black, apical margin of black slighty arcuate medially, third segment with dorsal black arcuate area narrowly connected laterally with large lateral spot, fourth and fifth segments with discal lunate black areas extending two-thirds distance to apical borders, separated from small lateral spots, sixth with lunate median black spot; terminalia orange, narrow, apical half of lateral lobes of ninth tergite rather abruptly narrowing to tip, clothed with yellow pile. *Undersurface* of thorax black covered with grey pollen, abdominal sternites yellow, sparsely pilose; front femora with proximal two-thirds black, middle femora yellow with proximal black stripes on front and hind margins extending to distal third, hind femora black except for subdistal yellow band, tibiae, tarsi, macrochaetae and pile yellow. Length 20 mm., width 4.7 mm. (Plate 2, Fig. 6).

Female.—Unknown.

Holotype male, Number 4721, Calif. Acad. Sci., Ent., collected in the Panamint Mountains, Inyo County, California, May 29, 1937. The writer is pleased to name this species in honor of Dr. T. G. Aitken who gave the specimen to the writer for description and loaned numerous other specimens during the course of these studies.

Judging from the small size, narrow terminalia and widely separated compound eyes it would appear that this species is somewhat intermediate between the *trochilus-terminatus* group and the *xanthos-painteri group*. With the former group it agrees in the wide vertex of the head, narrower form and slender terminalia and with the *xanthos-painteri* group by its small orange terminalia, small size, and general appearance. Its closest relative appears to be the species to follow and the differences will be given in the discussion of that species. The markings of *R. aitkeni* will serve to distinguish it from all other species.

Rhaphiomidas abdominalis n. sp.

Male.—Relatively small, narrow; thorax moderately clothed with yellow pile; abdomen yellow with median dark markings on segments two to five; lateral lobes of ninth tergite orange. *Head* with front densely clothed with yellow pile; compound eyes widely separated; antennae with first and second segments brown and yellow, macrochaetae yellow, third segment orange, elongate; mouthparts about one-half length of body. *Thorax* (damaged) with moderately dense yellow pile, macrochaetae yellow; scutellum with yellow pile and macrochaetae. *Abdomen* moderately clothed with yellow pile; segment one with base brown, thickest medially, apical yellow portion widest laterally, segment two with basal half brown, medially produced nearly at right angles, not attaining apex of segment, segments three to six with median basal spots; terminalia narrow, lateral lobes of ninth tergite evenly converging apically, densely clothed with yellow pile, ventral margin with shallow depression before apex, color yellow. *Legs* with front femora, tibiae and tarsi yellow, middle and hind legs yellow with brown or black macrochaetae. Length 20 mm., width 4.7 mm (Plate 2, Fig. 5).

Female.—Unknown.

Holotype male in the collection of the Museum of Comparative Zoology, Cambridge, Mass., collected at Colton, San Bernardino County, California, August 16, 1888, by F. A. Eddy. One male paratype from California, August 25, (C. W. Johnson) in the writer's collection. The paratype specimen was apparently killed before hardening but differs from the holotype only by its larger size. Length 23.2 mm., width 5 mm.

This species is most closely allied to *Rhaphiomidas aitkeni* Cazier but differs by having the pile yellow rather than grey, the abdominal markings angulate rather than lunate, the lateral lobes of the ninth tergite larger and gradually rounded to apex instead of small and angulate at middle and by having the macrochaetae of middle and hind legs black rather than yellow.

Rhaphiomidas parkeri n. sp.

Male.—Medium sized, relatively narrow; moderately densely clothed throughout with grey pile; abdominal segments black with narrow, apical, transverse, yellow band on dorsum of segments two, three and four; terminalia nearly cylindrical, ninth tergite with lateral lobes bicolorous, black bordered with orange. *Head* slightly wider than anterior angles of thorax; vertex and front densely clothed with grey pile; ocelli white, convex, compound eyes separated from lateral ocelli by at least the width of an ocellus; antennal segments one and two black, clothed with long grey pile, third segment glabrous, orange; palpi grey at apex, brown basally, pilose. *Thorax* black, grey pollen marginal and in two parallel, longitudinal, discal bands, separated by more than their own widths; entire surface rather densely clothed with long grey pile; posterior lateral margins of mesothorax and scutellum with long grey setae; wings with anal cell closed. *Abdomen* narrow, gradually tapering to terminalia, moderately densely clothed with grey pile; first, fifth, sixth and seventh segments black throughout, segments two, three and four with membranous apical edges yellow, bands narrowed laterally; terminalia subcylindrical, clothed throughout with grey pile, lateral lobes of ninth tergites bicolored black narrowly margined with orange, ninth sternite black, gonostyles orange, extending to apex of lateral lobes of ninth tergites. *Undersurface* moderately clothed with grey pile, especially dense on coxae; legs with macrochaetae grey, hind legs with femora and tibiae black, front and middle legs with tibiae and distal spot on femora orange; abdominal segments black except for yellow distal margins on segments two, three and four. Length 22 mm., width 5 mm. (Plate 2, Fig. 11).

Female.—Similar to the male but differing in the usual sexual characters and by having the grey pile on the fourth abdominal segment retrorse, segments five, six and seven with retrorse black pile, and by having the hind tibiae yellowish-brown rather than black. Length 22.0 mm., width 5 mm.

Holotype male, allotype female in the author's collection, taken at Blythe, Riverside County, California, April 18, 1939, by F. H. Parker in whose honor the author is pleased to name the species. Sixteen male and twelve female paratopotypes deposited in the collections of the California Academy of Sciences, R. H. Painter, F. H. Parker, T. G. Aitken and the author.

Rhaphiomidas parkeri is remarkably uniform in coloration, pilosity, size and shape in the type series, all specimens agreeing very well with the holotype. It is apparently only distantly related to any of the other species as its terminalia show a departure not exhibited by other members of the genus. The inner concave surface of the lateral lobes of the ninth tergite and the elongate gonostyles will serve to separate it from any other species. In general appearance it resembles *R. trochilus* (Coq.) but can at once be distinguished by its smaller size and the grey macrochaetae on the legs, in addition to the characters given above. From *R. aitkeni* Cazier it can be separated by the abdominal markings and subcylindrical terminalia.

The following biological notes on this species were kindly supplied by Mr. Parker. On April 18, 1940, at a golf course on the mesa near Blythe, California, specimens of *R. parkeri* were observed on the ground and in small shrubs where creosote bush cover was dense. The females would alight in sheep tracks or other depressions in the soft sand, work the abdomen into the sand, extending it about twice its normal length until the wings were flat on the ground and the abdomen assumed a vertical position. If undisturbed the female presumably laid an egg, then removed the abdomen from the sand and flew to another depression a few inches to several feet away and repeated the operation. Each "oviposition" required from one to two minutes to complete. Upon the removal of the abdomen, the sand filled the hole making it difficult or impossible to recover the eggs laid. These observations were made in the afternoon (3:30-7 p.m.) after the temperature started to drop but the actions may have taken place earlier, although, during the hotter portions of the day the flies were to be found mostly in the shrubs. Males were very abundant but were more difficult to obtain. Copulation took place at every opportunity, the males pursuing the females whenever the latter flew over or near them. Only one specimen was observed to fly to a sand verbena and extend its proboscis into the flower, hovering meanwhile as do the sphingid moths. Subsequent attempts to obtain eggs and larvae from this locality have proved fruitless. Several species of *Apiocera* were abundant in this area but were apparently confined to open areas and were not taken on shrubs.

Rhaphiomidas acton Coquillett

Rhaphiomidas acton Coquillett, 1891, West Amer. Sci., **7**:85, male; Townsend, 1895, Proc. Cal. Acad. Sci., (2) **4**:602; Painter, 1936, Bul. Univ. Kans., **37**:188.

Male.—Rather large, robust; pile and macrochaetae yellow; abdomen orange; lateral lobes of ninth tergite orange, large and robust. *Head* densely clothed with erect yellow pile; compound eyes widely separated at vertex; antennae black above, third segment orange beneath, macrochaetae on segments one and two yellow; mouthparts slightly longer than one-half length of body. Thorax densely clothed with yellow pile, lateral and posterior macrochaetae yellow; scutellum with yellow pile and macrochaetae. *Abdomen* rather densely clothed throughout with yellow pile; first segment black throughout, second with median V-shaped basal dark spot, third, fourth and fifth with median basal dark spots which get progressively larger apically; terminalia with lateral

lobes of ninth tergite orange clothed with yellow pile, ninth sternite orange, gonostyles projecting slightly beyond the middle of the lateral lobes of ninth tergite. *Undersurface* densely pilose; legs with femora brown basally, apically yellow, tibiae and tarsi yellow, tibial macrochaetae yellow, venter of posterior tarsi with double row of short, stout, black, spines, tibiae with single row on inner surface. Length 22 mm., width 6 mm. (Plate 2, Fig. 1).

Female.—Closely resembling the male except for the usual sexual differences and shorter, more sparse, abdominal pile. Length 25 mm., width 8 mm. (Plate 2, Fig. 2).

Type locality: Northern part of Los Angeles County, California, July.

The species has been collected in Riverside County, San Bernardino County and Los Angeles County of southern California and is apparently rather widespread.

Rhaphiomidas acton appears to be the most polymorphic member of the genus. None of the other described species shows such variation in size, color and markings as does *R. acton*. Perhaps future workers will find it necessary to break up the present species, as now known, into a number of subspecies or varieties. The material available at present does not, however, justify such a splitting of this variable species.

The pile varies from grey to yellow, the third antennal segment grades from predominantly black to completely orange, the abdominal markings are lacking or represented by median dorsal spots of varying sizes, the lateral lobes of the ninth tergite are occasionally clothed with black pile and the ground color grades from orange to black narrowly margined with orange.

Rhaphiomidas maehleri n. sp.

Male.—Rather large, robust; thorax, abdomen and terminalia rather densely clothed with yellowish pile; abdominal segments two to six orange-yellow, median dorsal black spots on each segment; terminalia orange with yellow pile. *Head* with front densely clothed with yellow pile; compound eyes widely separated at vertex; antennal segments one and two black with narrow, yellow distal rims, sparsely clothed with long grey pile throughout, third segment orange except for base and apices of dorsum; palpi brown at base, grey apically, sparsely clothed with long grey pile. *Thorax* black, clothed with grey pollen, sides with wide dark area, disk with two narrow, parallel, proximate dark stripes extending from apical margin to basal third, surface rather densely clothed with yellowish pile, posterior lateral margins of mesothorax and scutellum with long yellow setae; wings hyaline, anal cell closed. *Abdomen* gradually tapering to terminalia, rather densely clothed with yellowish pile; first segment black with about apical half yellow, second segment orange except for basal third and mid-dorsal, basal, black projection, third segment orange except for middle diamond-shaped spot, narrowly connected to base, fourth, fifth and sixth segments the same as the third except that the black spots are progressively larger from base to apex, lateral margins of all segments orange; terminalia

robust, orange, gradually narrowing to apex, clothed with orange pile. *Undersurface* of thorax black clothed with grey pollen and long yellowish pile, abdominal sternites yellowish orange, sparsely pilose; front femora with base of inner surface black, outer surface and apical fourth orange, middle femora orange except for proximal black area on inner surface, hind femora with apical third and narrow ventral stripe orange, remainder brown, tibiae, tarsi, macrochaetae and pile yellow, inner surface of basitarsi of middle and hind legs with double row of short black spines, tibiae of middle and hind legs with irregular row of short black spines on inner surface. Length 25 mm., width 6.2 mm. (Plate 2, Fig. 3).

Female.—Differs from the male in the usual sexual characters, is longer and more robust; discal thoracic pile short; abdominal segments one to four with narrow basal black band, middorsum of each segment with posteriorly projecting triangular spot, connected to base, apical three-fourths of each segment pale orange-yellow; legs as in male except for the posterior pair which have pile largely black, macrochaetae yellow, ventral spines on basitarsi yellow. Length 28 mm., width 8.5 mm.

Holotype male number 4751, allotype female number 4752 (Calif. Acad. Sci., Ent.), collected at Phelan, San Bernardino County, California, June 26, 1937, by K. L. Maehler and J. H. Robinson. The writer takes pleasure in naming the species in honor of Mr. Maehler who presented to the writer the specimens from which the type was selected. Both sexes were collected as they visited the flowers of *Lupinus* sp. during the mid-day. Seventeen male and ten female paratopotypes deposited in the collections of M. T. James, R. H. Painter, K. L. Maehler, T. G. Aitken, K. R. Norris and the writer.

Additional localities include: Cushinbury Springs, San Bernardino County, August 19, 1934 (C. D. Michener); Cajon Valley, San Bernardino County, June 22, 1932 (C. M. Dammers); North Fork Bishop Creek, Inyo County, Elevation 5000 feet, July 2, 1927 (V. Duran).

This species is much less variable than *R. acton* Coquillett but is apparently most closely allied to it, differing chiefly in the sexually dichromatic condition. The female of *R. maehleri* is distinguished from that of *R. acton* by the transverse, banded abdominal markings and pale yellow color as contrasted with the spotted markings and orange color of *R. acton*.

Rhaphiomidas maculatus n. sp.

Male.—Large, robust; densely clothed with golden pile; thorax black; abdomen predominantly deep orange, maculations in the form of large, dorsal, black, abdominal spots. *Head* with front densely clothed with yellow pile; compound eyes widely separated on vertex; antennae black dorsally, venter and base of third segment brown, first segment one and one-half times length of second, third about one-third longer than first and second combined, setae on first and second segments yellow; palpi dark brown. *Thorax* black, brown pollinose, densely clothed with long yellow pile, posterior lateral margins of mesothorax and scutellum with long yellow setae. *Abdomen* densely clothed

with yellow pile which is longest on lateral margins; first segment black except for narrow orange stripe in middle laterally; second segment orange except for mid-dorsal black diamond-shaped spot, apically inverted, median triangle and small basal lateral triangle, third and fourth segments orange except for discal black diamond-shaped spot, larger on fourth, and black lateral basal angles; fifth segment orange with median, oblong, black basal spot, larger than that of fourth, sixth and seventh segments orange with middorsal black areas larger than that of fifth; terminalia robust, orange, lateral lobes of ninth tergite with rather deep subapical emargination on ventral edge, densely clothed with pile. *Undersurface* of thorax black, covered with grey pollen, abdominal sternites orange except for black median spots on segments four, five and six; femora black on basal two-thirds except for middle pair which have entire length of upper surface orange, tibiae and tarsi orange, macrochaetae and pile of all legs orange-yellow. Length 28 mm., width 7.2 mm. (Plate 2, Fig. 4).

Female.—Same as male except for darker brown pile on thorax, shorter abdominal pile, larger lateral abdominal black spots, longer and stronger hind legs and the usual sexual differences. Abdominal segments five, six and seven with retrorse black pile, brown dorsal area progressively larger on five and six, segment seven entirely brown dorsally. Length 26 mm., width 9 mm.

Holotype male number 4719, allotype female number 4720 (Calif. Acad. Sci., Ent.), collected at Coronado, San Diego County, California, June 20, 1890, by Dr. F. E. Blaisdell. Three male paratypes from Kearney Mesa, San Diego County, June 20, 1938 (W. P. Medlav), two of which are in the collection of the San Diego Museum of Natural History and one in the writer's collection. One female paratype from Torrey Pines, San Diego County, California, July 20, in the collection of the United States National Museum.

The paratype males differ from the holotype in having the abdominal pile less dense and shorter. One specimen has the abdominal markings reduced on the second segment and the lateral lobes of the ninth tergite have some black pile basally.

This species is apparently most closely related to *R. acton* and *R. maehleri* Cazier. From *R. acton* it can be separated by its darker color, longer and more dense pile and more extensive abdominal black markings. From *R. maehleri* it is easily separated by its darker color, larger black markings, darker and more dense pile and by its sexually monochromatic condition.

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The Genus Arundanus (Homoptera-Cicadellidae) in North America

Dwight M. DeLong

A previous paper[1] by the author in 1935 established the genus *Arundanus* to include a group of species previously described in *Thamnotettix* and *Chlorotettix* and collected from species of cane, *Arundinaria*. At that time several species were known from only one sex, particularly the female and in several cases the males were not available for obtaining diagnostic characters. Since that time the writer has had an opportunity to obtain a considerable amount of material from the Carolinas and certain of the Gulf Coast states. It has been possible to obtain an abundance of material of most of the species described and to thus complete a study of the male genital structures. The illustration of these characters will serve to assist others in the identification of these species.

The species of *Arundanus* are confined by the distribution of their specific food plants to the southeastern United States, and certain of them are apparently further limited in their distribution within that range. With few exceptions the eastern coastal species of the Carolinas seem to be different from those found in the areas occupied by the western range of this plant in Tennessee, Kentucky, southern Illinois and Mississippi. This difference in specific distribution may be due to specific differences of the *Arundinaria* or to climatic factors alone.

The first species of this group described, *A. shermani* (Ball), was from a single female specimen and no male has since been found which seems to belong to this species. Two distinct species of males have recently been collected, either of which might have been placed with this female. The fact that each has accompanying females neither of which quite agree with *shermani* leaves the decision almost impossible at this time and both species are being described in the present treatment since it may prove to be that neither of these is the male of *shermani*.

Key to Species

1 Vertex marked with dark transverse bands or spots below or above margin, or both 2

1' Vertex without dark bands or spots bordering margin 13

2 Without a distinct dark band below vertex margin, marked above with distinct spots 3

2' With a distinct band below vertex margin 4

3 Vertex strongly produced, marked with four distinct spots above margin....*arundineus*

[1] De Long, D. M. Ent. News **46**:180. 1935.

3' More bluntly angled, with four spots just above margin and a larger pair just posterior to marginal spots ..... *duplus*

4 Markings above vertex margin forming a regular or irregular dark band, spots when present elongate and usually connected 5

4' Marking above vertex in form of separate spots 11

5 Vertex strongly produced and angled, spots distinctly triangular, the pair at center with base of triangle either side of and parallel to median line..... *proprius*

5' Spots above vertex not distinctly triangular, usually rounded on margin along median line 6

6 Female last ventral segment appearing truncate, male where known with aedeagus with bifid pointed apex or with a pair of long spearhead pointed apices..... 7

6' Female last ventral segment produced, trilobate or excavated, male aedeagus either broadened near apex with a pair of separated converging processes or with a broad blade on dorsal portion 9

7 Vertex broad appearing almost rounded, line above vertex composed of elongated spots. Male not known ..... *shermani*

7' Vertex appearing more angularly produced, line above margin usually more uniform 8

8 Male aedeagus in ventral view tapered at apex to a bifid pointed tip..... *fastigatus*

8' Male aedeagus in ventral view divided near middle and produced forming a pair of long curved separated terminal process which cross at apex and have "spearhead formed" tips ..... *sarissus*

9 Female segment excavated with a small median sunken tooth. Male dorsal portion of aedagus broad and blade-like ..... *carolinus*

9' Female segment produced or lobate. Male dorsal aedeagus with narrow spine-like processes 10

10 Female segment strongly produced at center forming a broad produced lobe beyond lateral angles. Male aedeagus with short terminal processes beyond broadened portion ..... *latidens*

10' Female segment trilobate, male aedeagus less broadened near apex, with longer terminal processes, long terminal processes of styles and with longer spine-like processes on the dorsal portion of aedeagus ..... *marginellus*

11 Small, not exceeding 4.5 mm. in length, a narrow brown line beneath vertex margin curved around ocelli on outer margins and with four spots above margin ..... *parvulus*

11' Larger, 5 mm. or more in length, band beneath margin heavier not curved around ocelli 12

12 With conspicuous longitudinal orange bands on vertex and pronotum. Vertex with a pair of longitudinal dark dashes at terminus of these bands above margin ..... *rubralineus*

12' Without conspicuous longitudinal orange bands on vertex and pronotum with four small dark spots above margin ..... *crumbi*

13 Apex rather pointedly produced, without orange longitudinal bands on vertex and pronotum 14

13' Apex more bluntly angled, conspicuously marked with longitudinal orange bands on vertex and pronotum 15

14 Male uniformly orange in color, female uniform milk white. Female segment with produced membrane which is deeply broadly notched at center. Male with a short broad blunt ventral aedeagus and a pair of long blade-like structures on the dorsal aedeagus which are pointed at apex ..... *nacreosus*

14' Male and female yellow tinged with orange. Female segment broadly shallowly excavated with a slight U-shaped notch at center. Male ventral aedeagus with a pair of proximal pointed teeth at apex. Dorsal aedeagus broad curved upward and with a broad blunt apex ..... *flavotinctus*

15 Female segment truncate deeply narrowly incised at middle ..... *rubralineus*

15' Female segment deeply broadly excavated with median incision..... var. *excavatus*

Arundanus duplus n. sp.

Superficially resembling *crumbi* in coloration but with a pair of black spots behind the row above anterior margin. Length 4.5 mm.

Vertex produced, bluntly angled, as long at middle as basal width between eyes.

Color dull yellow, vertex with a row of four black spots between ocelli just above margin, the middle pair the larger. A large spot behind these on each side of middle and in a line with the anterior margins of the eyes. Two longitudinal orange brown stripes on vertex, six on pronotum. Elytra brownish with pale veins.

Genitalia: Male plates rather long, bluntly pointed, slightly concave on outer margins. Styles with short outwardly curved apical process. Aedeagus in lateral view broadened at middle, narrowed toward apex with the apical third bent abruptly dorsally, anterior margin slightly produced just before narrowed, bluntly pointed apex.

The styles resemble those of the species of *Graminella* but the venation and external appearance are more typical of species of *Arundanus*.

Holotype male collected at Fulton, Mississippi, June 15, 1933, by D. W. Grimes.

Arundanus arundineus DeLong

Arundanus arundineus DeLong, Trans. Amer. Ent. Soc. **52**:91, 1926.

Resembling *proprius* in coloration but with spots above pale margin, smaller, not contiguous and without a dark band beneath the pale margin.

Vertex bluntly angled, about one-fourth wider between eyes at base than median length.

Genitalia: Female last ventral segment deeply rounded notched on median half. Male aedeagus with the ventral portion rather short and curved dorsally at the apex forming a blunt tip. Dorsal portion extending from base, longer than ventral portion, slightly enlarged at apex which is truncate and serrate.

Known only from Tennessee, Illinois and Kentucky.

Arundanus proprius (DeLong)

Thamnotettix proprius DeLong, Ohio Jour. Sci. **18**:238, 1918.

In coloration more closely resembling *shermani* but with a strongly produced, angled vertex. The vertex margin is pale, bordered beneath by a uniform black band and above by a band composed of three large triangular spots. The central pair are largest and decidedly separated.

Vertex a little wider between eyes at base than median length.

Genitalia: Male plates long and narrow, bluntly pointed. Aedeagus in lateral view curved dorsally at apex and enlarged into a half spearhead, the enlargement being on the caudal margin. Style with a short, outwardly curved, apical process.

This species is known only from the holotype male which is unique in both color markings and male genital structures and was collected in Tennessee.

Arundanus shermani (Ball)

Thamnotettix shermani Ball, Can. Ent. **35**:230, 1903.

This is a broad headed species with a pale marginal band bordered by a narrow brown band beneath and an irregular dark band above, the latter composed of three triangular spots each side of middle.

Vertex broad, almost rounded at apex, one third wider between eyes at base than median length.

Genitalia: Female last ventral segment appearing truncate. The male of this species has not been definitely determined from material which has been examined.

Arundanus fastigatus n. sp.

Resembling *latidens* in general appearance but with vertex more produced and a more broken brown band above margin. Length 5.5 mm.

Vertex rather strongly produced and bluntly angled, a little wider between eyes at base than median length.

Color orange to brown, vertex margin wihte, bordered below by a narrow black line and above by a slightly broken or irregular brown line composed of elongated spots. Elytra smoky brown, veins paler.

Genitalia: Female last ventral segment truncate or sinuate. Male plates long, bluntly pointed. Styles with apical portions rather long, parallel margined, rounded at apex. Ventral portion of aedeagus pointed at apex and appearing bifid in ventral view. Dorsal portion with a short median, rather broad plate and a rather long process either side which is narrowed to form a long slender sharply pointed upturned apex.

Male holotype, female allotype and male and female paratypes from Carolina Beach, N. C., Junt 8 and 9, 1940, and Wilmington, N. C., Junt 9, 1940. Collected by Mr. and Mrs. George Wene and the writer.

Arundanus sarissus n. sp.

Resembling *latidens* in general appearance but with brown band above pale margin more broken and uneven. Length 4.5-5 mm.

Vertex bluntly angled, about one-third wider between eyes at base than median length.

Color orange-yellow, vertex margin white, bordered below by a black band, and above by a brown band which is formed by three contiguous elongated spots, the largest of which are either side of the interruption at the middle. Veins of elytra almost unicolorous, not conspicuous.

Genitalia: Female last ventral segment appearing truncate. Posterior margin roundedly excavated, the central portion of which is filled to the distance of the

lateral angles with what appears to be an underlying membrane. Male plates tapered to bluntly pointed apices. Styles with apical portions rather long, parallel margined, pointed on inner apical margin. Aedeagus with ventral portion branched at about half its length to form two long curved apical processes which are spear-like at their apices. The dorsal portion arises near the base and is composed of a short median process and a pair of long slender processes extending dorsally.

Male holotype, female allotype and male and female paratypes collected at Carolina Beach, N. C., Junt 8 and 9, 1940, and at Wilmington, N. C., June 9, 1940, by Mr. and Mrs. George Wene and the writer.

Arundanus carolinus DeLong

Arundanus carolinus DeLong, Ent. News **46**:181, 1935.

Similar to *latidens* in markings and general appearance but with more produced head and distinct genitalia.

Vertex bluntly angularly produced, a little wider between the eyes than median length.

Color brown tinged with orange, vertex margin yellow, margined above and below with a waved black line. The line above often broken into elongate dashes.

Genitalia: Female last ventral segment with posterior margin broadly concavely rounded with a short, broadly rounded produced tooth at center. Male aedeagus with apex curved dorsally. At the base a large dorsal portion arises which in lateral view is broad, blade-like, curved and broadened before the acutely pointed apex.

Known to occur only in North and South Carolina.

Arundanus latidens DeLong

Arundanus latidens DeLong, Ent. News **46**:182, 1935.

A brownish species with a pale margin bordered above and below with a dark brown line. The band above is continuous but waved and interrupted at middle.

Vertex broadly bluntly angled, about one-fourth wider between eyes at base than median length.

Genitalia: Female segment with a broad median produced tooth which is produced decidedly beyond the rounded lateral angles of the posterior segment. Male aedeagus in ventral view roundedly enlarged before apex with a pair of rather long narrow converging apical processes. In lateral view the aedeagus rounds at apex to a pointed tip. Near the base a short dorsal process arises with a pair of rather long slender spines protruding in the dorsal chamber. The apex of the style is short with a truncate tip which is slightly broadened.

This is a very common species in the North and South Carolina areas of *Arundinaria* but has not been collected in the other states where this food plant occurs.

Arundanus marginellus DeLong

Arundanus marginellus DeLong, Ent. News **46**:181, 1935.

A broad headed species similar in form and appearance to *shermani* but with a trilobate female segment.

The vertex is orange in color. The margin is white with a black band just above and below. The band above is broader either side of middle then tapers to a very narrow line above ocelli. Veins of elytra white as in *shermani*.

Genitalia: Female last ventral segment with lateral angles produced and rounded, between which the posterior margin is excavated either side of a median produced tooth which is broad and often slightly bifid at apex, thus giving the posterior margin a trilobate appearance. Male styles with long parallel margined apices which are not broadened at apex as in *latidens*. Aedeagus similar to that of *latidens*, broadened before apex with two long spine like processes protruding at apex.

Known only from Tennessee, Illinois, and Clemson College, South Carolina (O. L. Cartwright).

This species is similar in structure to *latidens*. The male styles have longer apical structures and the aedeagus, although the same type, is less expanded just before apex and the apical pointed processes are decidedly longer. The paired elongated spurs on the dorsal portion of the aedeagus are also longer than the similar processes in *latidens*.

Arundanus parvulus DeLong

Arundanus parvulus DeLong, Ent. News **46**:182, 1935.

A small orange colored species without definite color markings except a narrow pale waved marginal band between a narrow ventral marginal line, which is waved, and a few faint markings above margin, especially a pair of faint spots at middle and a faint spot next each ocellus.

Vertex bluntly angled about one-third wider between eyes than median length.

Genitalia: Female last ventral segment with posterior margin broadly, rather deeply concavely rounded. A produced membrane appears as a convexly rounded portion of the segment at middle. Male plates long slender, bluntly pointed at apex. Style with a long apical portion which is broadened at truncated apex. Aedeagus rather short and thick with apex enlarged and upturned. At the base is a short broad process extending dorsally with a long slender spine either side which extends caudally.

Allotype male collected at Carolina Beach, N. C., June 8, 1940, by the writer. Known only from North and South Carolina.

Arundanus crumbi (DeLong)

Thamnotettix crumbi DeLong, Tenn. St. Bd. Ent. **17**:181, 1916.

In form and appearance resembling *flavotinctus* but with distinct color markings.

Vertex margin marked with a broad brown waved band and with four rounded almost equidistant brown spots between eyes just above margin. Vertex sharply angled about one-fourth wider between eyes than median length.

Genitalia: Female last ventral segment with posterior margin broadly angularly excavated, the apex of notch slightly rounded. Male plates long and narrow, bluntly pointed. Aedeagus in ventral view with ventral portion narrowed and forming two long-spine teeth. In lateral view narrowed to a sharp pointed apex. The dorsal portion is curved dorsally, being almost the same width throughout and truncate at apex.

Known from Tennessee and Illinois, where it occurs abundantly upon cane. It has been taken more recently at Clemson College, South Carolina, by Cartwright. It has not been collected on the low coastal plain.

Arundanus flavotinctus (DeLong)

Thamnotettix flavotinctus DeLong, Tenn. St. Bd. Ent. Bull. **17**:821, 1914.

With a sharply angled vertex, one-fourth wider between eyes than median length, orange-yellow with very faint if any color markings.

Genitalia: Female last ventral segment shallowly rounded, notched on median half. Lateral angles broadly rounded. Male plates long and slender, rounded at apices. Styles with rather long almost parallel margined apical portions which are divergent and enlarged on inner margins at apex. Aedeagus with ventral portion narrowed at apex to form a pointed tip in lateral view, or an apex with a pair of long spine-like teeth in ventral view. Dorsal portion of aedeagus broad, bent abruptly dorsally at about half its length, broadened and with a blunt serrate apex.

Known only from Tennessee and Illinois, and one specimen is at hand from Clemson College, South Carolina (Cartwright).

Arundanus rubralineus DeLong

Arundanus rubralineus DeLong, Ent. News **46**:181, 1935.

Distinct in color with a broad, bluntly angled vertex, about one-fourth wider between eyes than median length. Margin of vertex usually not banded and usually without any dark markings. Vertex marked only by a pair of broad longitudinal orange-red stripes, occasionally a black line on margin. Elytra tinted with orange and with white stripes along claval area. Veins pale.

Genitalia: Female last ventral segment with posterior margin sinuately truncate or emarginate with a narrow incision at center extending two-thirds the distance to base. In one specimen this incision is widened to form a deep V-shaped notch. Male plates with broad bluntly rounded apices. Styles with long parallel margined apices which are two-thirds the length of the basal portion. Aedeagus with two portions. The ventral portion long, rather narrow and tapered to a pointed apex. The dorsal portion arising at the base is broader and narrowed near apex to a slender pointed apical process. This bears on the dorsal portion near the base a pair of long processes which extend dorsally.

Allotype male from Biloxi, Miss., collected June 11, 1933, by Mr. D. W. Grimes.

Arundanus rubralineus var. **excavatus** n. var.

In color, form and appearance resembling *rubralineus* but with different female genitalia. Length 5 mm.

Vertex broadly, bluntly angled and with two longitudinal orange-red stripes on vertex.

Genitalia: Female last ventral segment with prominent lateral angles between which the posterior margin is broadly deeply excavated more than half way to base with a short V-shaped notch at middle of excavation, the apex of which is surrounded by a black spot.

Holotype female and paratype females collected at Fulton, Miss., by D. W. Grimes in June 1934.

Although the female segment appears entirely different from *rubralineus*, it is not possible to determine with the present material whether the female character is variable or if this may be a distinct species.

Arundanus nacreosus (Crumb)

Chlorotettix nacreosus Crumb, Anns. Ent. Soc. Amer. **8**:196, 1915.

Distinct in color with dimorphic sexual coloration. Male uniform orange and female milk white without definite color markings.

Vertex bluntly angled, one-third wider between eyes at base than median length.

Genitalia: Female last ventral segment appearing four lobed. The posterior margin is deeply roundedly notched at middle and either side of a pair of median roundedly produced lobes. Lateral angles produced forming the outer lobes. Male plates short, apices blunt, rounded. Aedeagus with ventral portion short and broad, apex blunt in lateral view. Dorsal portion composed of a pair of long blade-like processes which exceed both plates and pygofers.

Known only from Tennessee, Illinois and Kentucky, until recently when it was collected at Clemson College, South Carolina, by Cartwright. It apparently does not occur on the low coastal plain area of the Carolinas.

Ohio State University,
Columbus, Ohio.

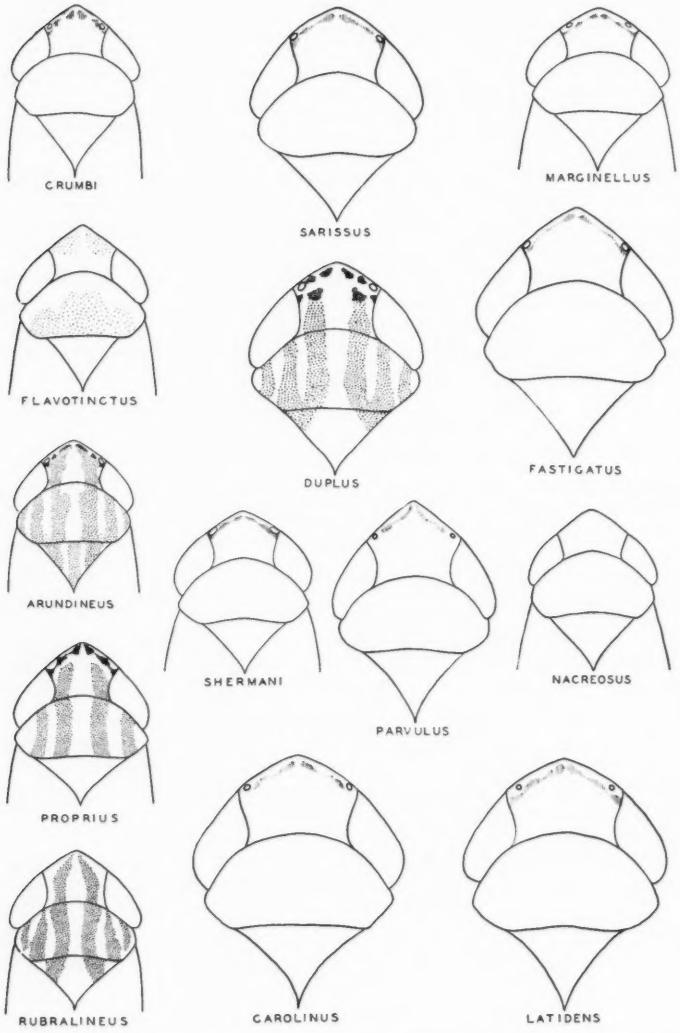


PLATE 1. Dorsal view of head and pronotum of species of *Arundanus* as named.

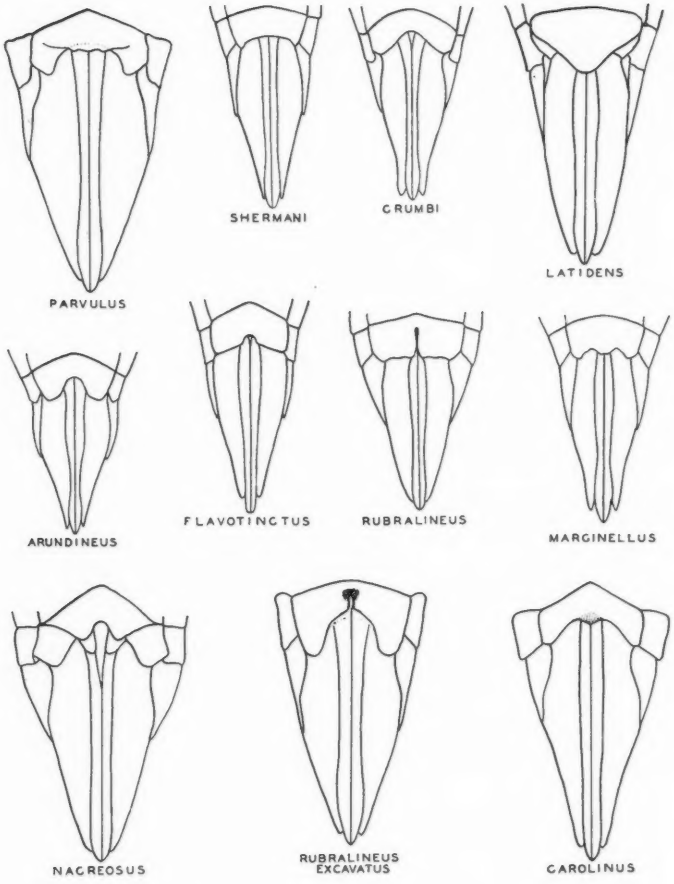
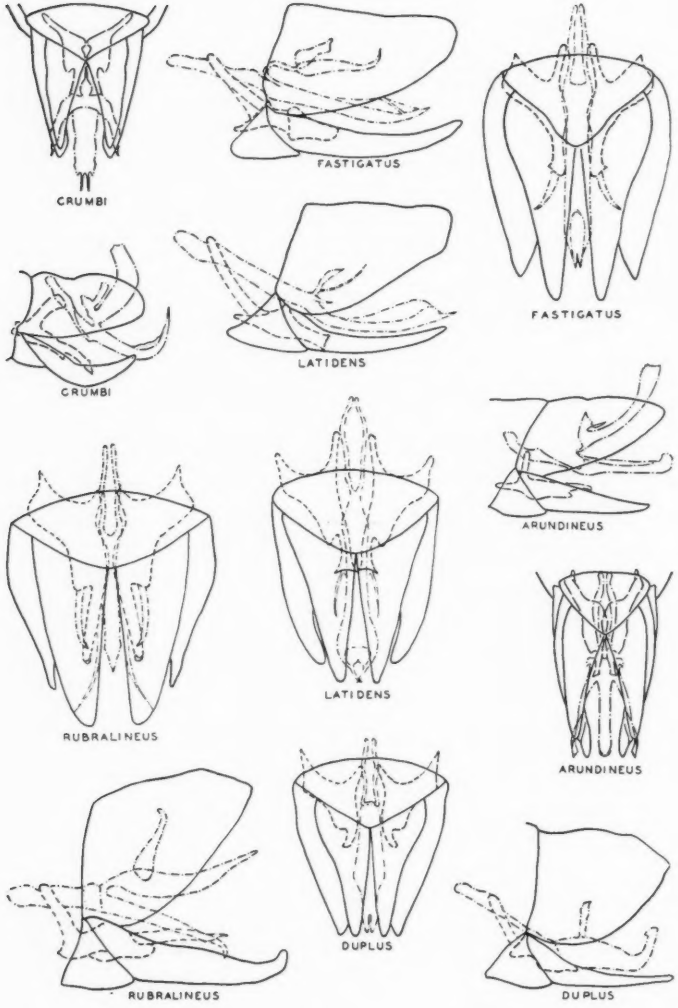
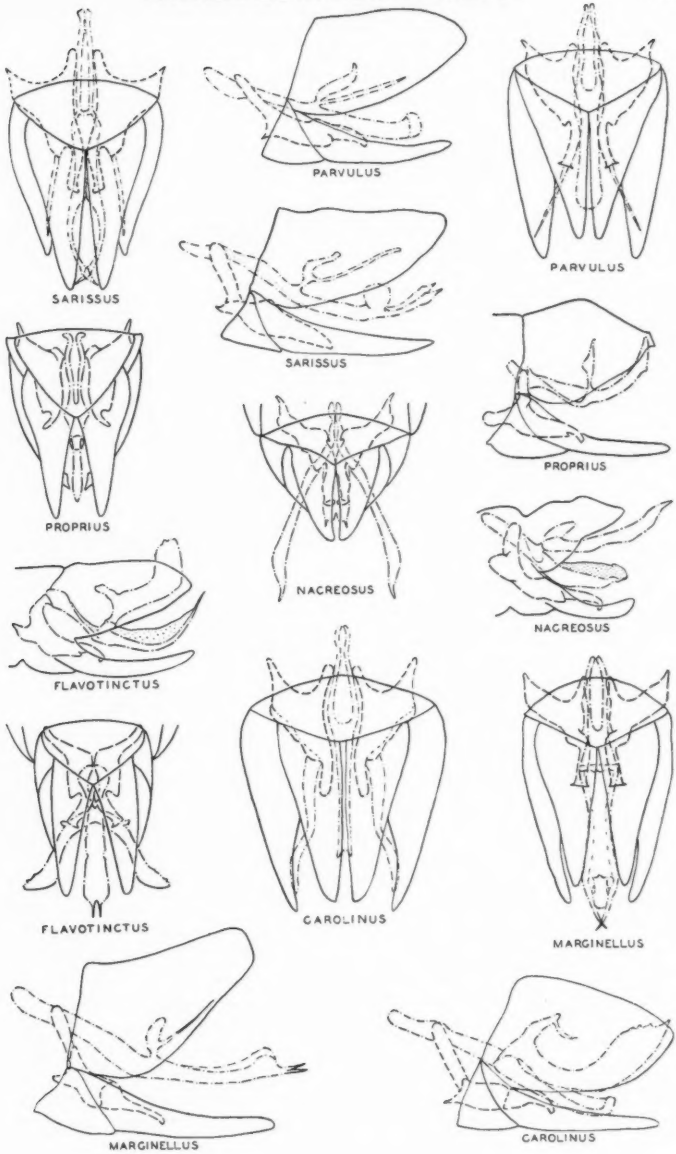


PLATE 2. Last ventral segments of females of species of *Arundanus* as named.



PLATES 3 and 4. Ventral and lateral views of the apical segments of the males of species of *Arundanus* as named, showing the genital structure in position.


SARISSUS
PARVULUS
PARVULUS
SARISSUS
PROPRIUS
PROPRIUS
NACREOSUS
NACREOSUS
FLAVOTINCTUS
FLAVOTINCTUS
CAROLINUS
MARGINELLUS
MARGINELLUS
CAROLINUS

Habits of Land Mollusca at Rensselaerville, Albany County, New York

William Marcus Ingram

The following observations were made between June 15 and September 1, 1940, on the Edmund Niles Huyck Preserve, Rensselaerville, Albany County, New York. The preserve is a tract of land of some 500 acres situated in the Helderberg Mountains; the altitude varies from approximately 1500 to 1750 feet. The climax forest is beech-hemlock.

Data gathered from field study concern: (1) land snail hibernation, (2) atypical feeding habits of land mollusks, and (3) types of trees selected by land mollusks in tree ascension after rains.

Land Snail Hibernation

During a cold spell lasting from August 19 through August 26 information was gathered showing that stylomatophorous pulmonate mollusks may hibernate for a period of at least a week during the Serotinal aspect. With renewed higher temperatures dormant mollusks again become active before entering into winter hibernation.

August hibernation data with a discussion of the types of aperture stoppers formed are presented here for 8 species of land mollusks, namely: *Succinea ovalis* Say, *Anguispira alternata* (Say), *Triodopsis albolabris* (Say), *Triodopsis dentifera* (Binney), *Triodopsis tridentata* (Say), *Mesomphix cupreus* (Rafinesque), *Ventridens intertextus* (Binney), and *Haplotrema concavum* (Say).

As a criterion to determine whether or not snails were hibernating, the presence or absence of an epiphragm or other aperture plug was used. If an aperture stopper was present it was concluded that hibernation was taking place; the absence of such a stopper was considered evidence that the animals were not in hibernation. Concerning the preparation for extended winter hibernation Baker (1902) states, "In October or November the snail ceases to become active and prepares to hibernate. This it does by secreting a membrane and placing it over the aperture." Binney (1885) describes epiphragm formation, referring to North American land snails in general as follows, "The animal being withdrawn into the shell, the collar is brought to the level with the aperture, and a quantity of mucus is poured out from it and covers it. A small quantity of air is then emitted from the respiratory foramen, which detaches the mucus from the surface of the collar, and projects it in a convex form, like a bubble. At the same moment, the animal retreats farther into the shell, leaving a vacuum behind itself and the membrane, which is consequently pressed back by the external air to a level with the aperture, or even farther, so as to form a concave surface, where, having become desiccated and hard, it

remains fixed. These operations are nearly simultaneous, and occupy but an instant."

Field collecting every day from August 12 to August 18, the period immediately preceding that of snail hibernation, brought no evidence that any of the above species showed any tendency to hibernate. During this period the mean temperature was 69.83 degrees.[1] The mean low temperature was 59.25 degrees, and the mean high temperature 80.42 degrees. The highest temperature for any day was 86 degrees and the lowest temperature 52 degrees. During the next week, from August 19 through August 26, the mean temperature dropped to 59.07, a decrease of 10.76 degrees from the preceding week. The mean high temperature was 73.57, a decrease of 6.85 degrees, and the mean low temperature was 44.57 degrees, a decrease of 14.68 degrees. The highest temperature for any day was 72 degrees and the lowest 37 degrees.

It was on August 21 that snails were first collected with epiphragms at their apertures. On this date the maintenance of low temperatures of from 43 to 44 degrees for a period of approximately ten hours caused large numbers of the various species mentioned to go into hibernation. Temperatures of from 40 to 50 degrees continued throughout the week. The longest cold spell during the period of from August 19 through August 26 occurred on August 24, when the temperature varied from 47 to 49 degrees for 13 hours. Between August 19 and August 27 the highest temperature, that of 72 degrees, was maintained only for one hour on August 23. Snail activity was again resumed

1 Fahrenheit temperature readings.

TABLE 1.—Snail Hibernation Data.

Species of Snail	Total no. observed	No. in Shelter1	No. in Open	Partial Epip. or Plug	Complete Epip. or Plug	No Epiphragm
Haplotrema concavum	6	6	0	0	6	0
Succinea ovalis	1	1	0	1	0	0
Anguispira alternata	1	1	0	0	1	0
Triodopsis albolabris	20	17	3*	8	7	5x
Triodopsis dentifera	4	3	1°	4	0	0
Triodopsis tridentata	3	3			2	1
Mesomphix cupreus	6	6		2		4–
Ventridens intertextus	7	7		6		1
TOTAL	48	44	4	21	16	11

1. each column subsequent to "Total no. observed" represents the number of this total in shelter, in open, etc.

* one with complete epiphragm, 2 with incomplete epiphragms.

x 3 of the 5 active beneath humus.

° partial epiphragm present.

– all inactive.

on August 28, 29, and 30, with high temperatures being maintained between 60 and 75 degrees for several hours at a time. During the cold spell ten *Triodopsis albolabris* with epiphragms were brought into the laboratory in jars; by maintaining a temperature between 68 and 70 degrees for three hours all became active.

Of the 48 individuals collected during the period of from August 19 through August 26, 37 possessed epiphragms or partial aperture plugs, and 11 were without any type of aperture stopper (Table 1). Of these 11, four individuals *(Mesomphix),* though without aperture plugs, were dormant during the cold spell. These four were among marked snails, and no movement was observed until August 28. Another three *(Triodopsis albolabris)* of the 11 were actively crawling about beside logs sheltered by a cover of humus; three others, two *Triodopsis albolabris* and one *Triodopsis tridentata* formed no epiphragms but remained inactive beneath humus during the cold spell. One immature *Ventridens intertextus* was found active beneath humus.

The epiphragm-forming snails were *Haplotrema concavum, Triodopsis albolabris, Triodopsis tridentata,* and *Triodopsis dentifera.* In these species a membrane was generally secreted at the aperture, thus sealing the shell opening. The epiphragms either completely or partially covered the apertures (Table 1).

The epiphragms formed by *Triodopsis albolabris* were complete or partial; eight partial and seven complete ones were observed in the individuals studied (Table 1). These observations are in accord with those of Simpson (1901) who says of *T. albolabris,* "It is stated by nearly all writers on this subject that there is always a perforation in this membrane [Epiphragm] to allow for passage of air; but I have observed numerous cases where the membrane was entire." Two of the partial epiphragms had circular openings abutting the parietal wall of the aperture; four snails had irregular splits in the approximate centers of their epiphragms. This latter condition seemed to indicate that the epiphragms had been formed originally as complete structures, but on drying had contracted and thus split down their middles. In two other instances epiphragms existed only around the margins of the apertures. With both of these individuals the partial epiphragms served to cement the aperture to leaves on the forest floor. One had a beech leaf and the other a maple leaf cemented by the partial epiphragms firmly over the shell apertures. These leaves no doubt functioned as would a total epiphragm in giving nearly total protection to the animal. The writer attempted to shake the two cemented mollusks off their respective leaves but without success. When the two were finally pulled from the leaves a cracking sound resulted and portions of the leaves were pulled away with the mollusks.

Only one *T. albolabris* had a double epiphragm. This mollusk had had a hole poked in its shell 10 mm. back from the aperture lip; the animal had secreted an epiphragm at the aperture mouth and another one 10 mm. from the aperture over the break in the shell. Another *T. albolabris* possessed an epiphragm completely surrounding a hemlock cone, which had apparently become lodged in the aperture at the onset of cold weather. No effort had apparently been made to move away from the cone at the aperture mouth.

It was possible to lift this individual from the ground by using the cone as a handle without tearing the epiphragm.

Fecal strings between the body of retracted individuals of *T. albolabris* and the epiphragms were not uncommon, indicating that if the animal eats before going into hibernation the digestive and excretory processes continue for a short time at least. The release of fecal strings by hibernating snails between the body and the epiphragm is not recorded either by Baker (1902) or Binney (1885), who described the completely dormant state of hibernation. Baker (1902) states, "During hibernation the heart almost ceases to beat, and all of the functions of the body cease, the animal becomes torpid. . . ." Binney (1885) states that ". . . the state of torpor is adopted, during which the functions of digestion . . . are suspended, and all the secretions and excretions have ceased. . . ."

Concerning the position assumed by hibernating individuals of *T. albolabris* Simpson (1901) states, "During cold weather they hibernate, partially burying themselves in the ground, with the apex of the shell downward." This position was not observed in the 15 hibernating *T. albolabris* at Rensselaerville; the apical whorls of these individuals were directed upward with the aperture pointed toward the substratum. Binney (1885) also mentions burrowing by snails preparatory to hibernation, the mollusks finally resting with the aperture upward. Binney's statement is a general one referring to North American land snails. However, at Rensselaerville no snail was found buried in the soil, and in only one instance was a snail *(Triodopsis dentifera)* found lying on its apex with the aperture in the air. The nearest approximation to burrowing was the position of one *Mesomphix cupreus* which was found beneath a six-inch pile of maple leaf humus in contact with the ground. Whether more snails would be found in the positions described by Simpson and Binney later in the year, when winter hibernation had taken place, is not known.

None of the four individuals of *Triodopsis dentifera* possessed a complete epiphragm (Table 1). One of the epiphragms was pierced by a central hole 2 by 3 mm.; another covered only two-thirds of the aperture. The other two epiphragms had longitudinal slits down their centers as though contraction had occurred after the epiphragms had dried, the epiphragms originally being complete ones.

The complete epiphragms found on two *Tridopsis tridentata* were each firmly attached to the aperture lip over the one parietal and the two labial denticles (Table 1). The one *T. tridentata* without an epiphragm was taken from beneath humus.

If formation of the epiphragm may be used as a criterion of snail sensitivity to cold weather, data presented here would indicate that individuals of *Haplotrema concavum* respond more readily to cold than do the other species considered. All six individuals of *Haplotrema* had complete epiphragms formed. One possessed a double epiphragm. At the beginning of the cold spell this individual was apparently eating a young *Triodopsis albolabris;* rather than rid

itself of the shell of the prey the *Haplotrema* secreted an epiphragm around it, thus sealing the *Triodopsis* shell in its aperture mouth. Retiring further into its shell the *Haplotrema* then secreted another epiphragm behind the first.

The snails which formed aperture stoppers other than the epiphragm type formed by the above four species of snails were *Anguispira alternata, Succinea ovalis, Mesomphix cupreus,* and *Ventridens intertextus.* In these species with the exception of *Anguispira* the foot was seemingly used as a block to aid in closing the aperture.

The single *Anguispira alternata* had a plug of foamy mucus at the aperture of the shell. This plug completely blocked the aperture.

The two individuals of *Mesomphix cupreus* (Table 1) had the foot firmly pressed against the sides of the shell at the aperture. The exposed foot surface almost completely blocked the aperture mouth; in each individual the external foot surface appeared to be dry. From the margin of the foot a very fragile membrane extended to the shell surrounding the aperture opening. Thus a circular membrane not over .75 mm. in width covered the space between the foot and shell at the aperture. The one *Succinea ovalis* had an aperture stopper formed as in *Mesomphix* except that the circular membrane between the foot and the shell was incomplete, the membrane being absent on the parietal wall of the aperture.

The six individuals of *Ventridens intertextus* (Table 1) each had the foot at the aperture mouth, with a thin membrane from .10 to .25 mm. in breadth encircling the shell aperture. The circular membrane extended from the foot to the aperture, which, however, was not completely blocked owing to the incompleteness of the membrane.

Data included in this section show that certain land snails hibernate for short periods during cold weather in August; that such hibernating snails form incomplete or complete epiphragms or other aperture plugs; that before going into hibernation snails usually take shelter beneath cover, but do not dig themselves into the soil. The typical position of snails during brief hibernation periods shows the animals resting with the apical whorls directed upward with the aperture toward the substratum.

Atypical Feeding Habits of Land Mollusks

Observations of feeding activities indicate that certain herbivorous snails may become on occasion carnivorous scavengers; that certain snails may be attracted to and feed upon man-made food when it is placed in the snail's natural habitat; that one typically carnivorous snail shows herbivorous tendencies when deprived of its carnivorous diet; and that several species, when deprived of their natural diet, will feed on paper.

Concerning the carnivorous habits of herbivorous snails Binney (1885) in referring to North American land snails, states, "Those found in this country are generally supposed to be vegetable feeders, but nearly all of them subsist occasionally upon dead animal matter, of which they seem to be fond. . . . It is probable, therefore, that in their natural condition all of them at times

resort to animal food. . . ." During the course of field study on the preserve five instances of carnivorous scavenger feeding by purportedly herbivorous species of snails were observed. The scavenger species were *Zonitoides arboreus* (Say), one individual, *Triodopsis albolabris* (Say), three individuals, and *Triodopsis dentifera* (Binney), one individual.

The *Zonitoides* was found on a dead deer-mouse, *Peromyscus maniculatus gracilis* which had but recently been killed in a snap-back mouse trap. When found, this snail had filed through the cornea of the mouse's eye, and was feeding on the crystaline lens in the eye cavity, having filed a surface groove in this structure. A portion of this species' normal diet is listed by Baker (1939), who states, "In several places outside Illinois, *arboreus* has become an enemy to agriculture by feeding on tender vegetation, or by damaging the root ends as it does in Louisiana cane plantations."

One of the three *Triodopsis albolabris*, an immature individual, exposed to the direct rays of the sun, was observed feeding on a freshly killed Calliophorid fly. The snail had ventured to the upper surface of the humus covering the forest floor to feed upon the fly. When the writer first observed the snail it had already succeeded in penetrating the thoracic wall of the insect's body and was feeding on the organs within the thorax. Its head and anterior foot region could be seen moving back and forth as though it was attempting to clean out all of the edible organs in the fly's thorax. The posterior foot region was held firmly on the substratum, thus giving the snail purchase for the feeding operation.

The other two *T. albolabris* and the one *dentifera* were taken from different individuals of the above species of deer-mouse which had been killed in snap-back traps. One *T. albolabris* and the *T. dentifera* were feeding on corneas while the other *T. albolabris* was performing a similar function on a mouse's vent. Simpson (1901) referring to *T. albolabris* states, "I very much doubt that they are ever carnivorous when furnished with an abundance of vegetable food." Carnivorous tendencies were shown in the three *T. albolabris* listed here even though an apparent abundance of vegetable food was present in the vicinity.

In the course of trapping for small mammals with snap-back traps peanut butter was often used as bait. During the summer 25 individuals of land pulmonates representing five species of snails and one species of slug were found on the trap pans feeding on the peanut butter. The snail species were *Triodopsis albolabris* (Say), *Mesomphix cupreus* (Rafinesque), *Triodopsis dentifera* (Binney), *Anguispira alternata* (Say), and *Zonitoides arboreus* (Say); the slug was *Philomycus carolinianus* (Bosc). Of these species *T. albolabris* seemed especially to relish peanut butter. Furrows in the surface of peanut butter 20 mm. long were often made by this species.

Three individuals of *Haplotrema concavum* (Say) were placed in a large vial and left for 28 days without their natural food. When these were first placed in the vial a locality label 10 by 30 mm., cut from an index card, was deposited therein with the snails. When the snails were examined on the twenty-eighth day only a few scraps of the locality label remained. A number

of white fecal masses varying from the normal brown color indicated that during the period of enclosure the snails had been feeding on the label. At this time the leaves of the sensitive plant, *Impatiens* sp., were placed in the vial with the snails. After three days the snails were again examined; the leaves of the sensitive plant had been partially consumed. No cannibalistic inclination occurred amongst the three *Haplotrema* during their 31-day fast from their customary diet of other snail species. When these three individuals were fed with *T. albolabris* and *M. cupreus* no inclination to feed upon available index card fragments or sensitive plant leaves was ever observed. The predatory *Haplotrema* was observed in the field feeding upon five species of snails. The following snails seem to constitute the natural diet of *H. concavum* on the E. N. Huyck Preserve, *Triodopsis albolabris, T. dentifera, Mesomphix cupreus, Zonitoides arboreus,* and *Anguispira alternata.*

In addition to *Haplotrema* the following species fed on index cards, *Triodopsis dentifera, T. albolabris,* and *Stenotrema fraternum* (Say).

Trees Selected by Land Mollusks in Tree Ascension after Rains

Two writers (Simpson 1901, Baker 1939) state that after rainy periods during the summer months snail collecting is extremely profitable. Following this advice the writer made two collecting trips in the climax beech-hemlock forest on the E. N. Huyck Preserve. Collecting efforts were confined to mollusks on the trunks of trees. As soon as the field work was begun it was observed that mollusks were far more numerous on beeches than on hemlocks; therefore data were kept on the number of mollusks respectively on each tree species, the dominant beeches and hemlocks as well as the less numerous maples and ashes.

Of the 70 mollusks gathered from tree trunks on the two rainy days only three were taken from hemlocks, although 90 of these trees were carefully searched for mollusks. Three of the total of 70 were collected from maple, five from ash, and 59 from beeches. The species of mollusks that were on the trunks of these trees were: *Philomycus carolinianus* (Bosc), 45 on beeches, two on hemlocks; *Triodopsis dentifera* (Binney), one on a hemlock; *T. albolabris* (Say), 14 on beeches, two on a maple, and five on an ash; and *Anguispira alternata* (Say), one four feet 6 inches up in the crotch of a maple.

The maximum height from which a mollusk was collected was 50 feet from the ground on a beech tree, where a *P. carolinianus* was found. Other extensive height records for individuals of this species were one at 35 feet, one at 30 feet, and one at 22 feet. The approximate average height from which slugs were collected was 9 feet above the ground. To measure the extreme heights listed above two calibrated poles lashed together were raised by hand above the observer's head and the position of the slug on the tree noted.

All of the *Philomycus* which were observed seemed to be stretched to their maximum extent both in the moving and quiescent states. Individuals which were collected on the ground under conditions of dryness seemed to be somewhat more contracted than individuals taken during rainy periods.

Before one of the collecting trips, at the time of a promised shower, the trees in a staked-off area were examined to see whether or not slugs were on

their trunks. No slugs were observed. Six hours after the rain had begun this area was again examined; one slug was 20 feet up a beech trunk, one 14 feet, one 12 feet, and one six feet. Several movement observations of *Philomycus* were made on dry days between the hours of 6 and 10 a. m. One individual was observed to move a total distance of 20 inches, one 7 inches, and one 9 inches during four hours. This movement was not directed in a fairly straight line as was the movement of *Philomycus* up trees during rainy periods, but was errant, with half circles and frequent rest involved in forward progress. It thus seems that during summer showers rate of movement is greatly accelerated in individuals of *Philomycus*. Too, with the coming of showers movement of *Philomycus* seems to be arboreal and directed rather than errant and terrestrial as it was found to be during the dry period of summer.

The typical habitat for *Philomycus* during dry periods seems to be beneath loose bark or in crevices in decaying logs, or beneath leaf humus. Only six individuals from a total of 247 individuals of *Philomycus* were ever collected on trees during dry periods in summer. These six slugs were gathered from within sap concavities on beech trees where branches had been broken away.

The maximum height from which an individual of *T. albolabris* was taken was 6 feet 6 inches on an ash trunk. None of the 21 individuals of this species which were observed during the rainy days was lower than a foot above the ground. From general observations it seems that, at least in the beech-hemlock association, individuals of this species typically become more active after rains during the summer, but that movement is generally terrestrial rather than arboreal as with *Philomycus*.

The preference of *Philomycus* during rains for beech trees over hemlocks is possibly due to one of two physical characters of hemlock trunks. Possibly the rough surface of the hemlock bark in addition to its acidity causes the slugs to avoid hemlock in favor of beeches. Roughness of surface apparently does not greatly affect individuals of *T. albolabris* in selecting trees to ascend during rains, since five of the 21 individuals taken during rainy periods were gathered from the rough bark ash. Hemlock trees were avoided by this species.

ACKNOWLEDGMENTS

Gratitude is expressed to members of the Scientific Advisory Committee and to the Preserve officers of the Edmund Niles Huyck Preserve. I wish to thank Mr. Frank Collins Baker of the University of Illinois and Mr. Calvin Goodrich of the University of Michigan for identifying several species of the snails cited here.

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Amphibians and Reptiles of the Duke Forest and Vicinity

I. E. Gray

The Duke Forest, comprising some five thousand acres of pine and hardwood stands, is located in Durham and Orange Counties in the Piedmont region in the north central part of North Carolina. The hilly terrain contains numerous small, rocky, spring-fed streams. The altitude is low and ranges between 280 and 650 feet above sea level. The relatively mild climate has an annual average maximum temperature of approximately 71 degrees and an annual average minimum temperature of approximately 48 degrees. Only occasionally does the temperature fall below zero, and severe weather usually does not last for more than a few days at a time. The soil seldom freezes to more than a few inches in depth. The annual rainfall varies, but for comparison with other regions, may be said to be approximately 42 inches.

The forest consists of three divisions. The New Hope Creek Division and most of the Durham Division drain into the Cape Fear River System through a fairly large stream, New Hope Creek, and its tributaries. The Eno River, a large branch of the Neuse River System, flows through the Hillsboro Division, and a small portion of the Durham Division contains creeks which flow into it. Thus the Duke Forest is drained by two different river systems.

Natural permanent ponds and lakes are scarce in North Carolina, so that pond-dwelling species have to make the most of temporary ponds, swampy areas, stream cut-offs, and artificial lakes formed by the damming of streams.

Herpetological records of the Duke Forest are essentially the records of the North Central Piedmont region of North Carolina. Brimley (1926, 1939-) gives the most complete herpetological records of any for the state, but he has omitted several species found in the Duke Forest that have not previously been reported from Durham and Orange Counties. Records for the state indicate that the herpetological fauna of North Carolina consists of 41 salamanders, 27 frogs and toads, 1 alligator, 8 lizards, 41 snakes, and 14 turtles (exclusive of sea turtles); a total of 132 species. Fifty-four species of these are known to occur in the Duke Forest; 12 salamanders, 12 frogs and toads, 5 lizards, 19 snakes, and 6 turtles. The collections which form the basis of this report were made during the ten-year period from October, 1930, to October, 1940. The scientific names are those used in the fourth edition of Stejneger and Barbour's Check List (1939). With the exception of the four-toed salamander and the horned toad, all species of amphibians and reptiles found in Durham County have also been found in Orange County.

Amphibia

Necturus lewisi (Brimley)—NORTH CAROLINA WATER DOG. While not common, this mud-poppy has been taken frequently by fishermen from the Eno River. It has not been found in New Hope Creek, which empties into a different drainage system than the Eno River.

Triturus viridescens viridescens (Rafinesque)—COMMON NEWT. The newt is common wherever there is standing water. The red eft land phase is found only occasionally, perhaps indicating that not all individuals of Triturus in this region go through the usual land stage in their development. In the hot months of summer, however, Triturus often leaves the shallow ponds and can be found nearby under logs and in other damp places.

Ambystoma opacum (Gravenhorst)—MARBLED SALAMANDER. This is a common species. Eggs are laid in September in bottom lands and in other places that will be flooded in winter. Active larvae may be taken from almost any temporary pond during the winter months.

Ambystoma maculatum (Shaw)—SPOTTED SALAMANDER. Other than in the breeding season, adults are not often taken, although this is by no means a rare salamander. Eggs are laid in January, February, or early March, depending upon weather conditions. They have been taken in early January following warm rains.

Eurycea bislineata cirrigera (Green)—SOUTHERN TWO-LINED SALAMANDER. This species is common in rocky creeks during the breeding season, which usually occurs during the last two weeks of March. In other seasons adults may be found near or at times even considerable distances from water. The eggs are attached to the under side of stones in the fast-running rocky streams and the female remains with them. Apparently two years are spent in the larval stage.

Eurycea longicauda guttolineata (Holbrook)—HOLBROOK'S SALAMANDER. This long-tailed salamander is not as common as the preceding species. It is usually found in the vicinity of a stream.

Pseudotriton montanus montanus (Baird)—BAIRD'S RED SALAMANDER. While this species is usually taken near streams, at times it may be found at considerable distance from water.

Pseudotriton ruber ruber (Sonnini)—RED SALAMANDER. This large salamander is usually found near streams. Often it lies in the damp creek beds, but not necessarily in the water. It has been taken on many occasions from muddy crayfish burrows along the banks of streams.

Desmognathus fuscus fuscus (Rafinesque)—DUSKY SALAMANDER. Apparently this is the only member of the genus *Desmognathus* that occurs in Durham and Orange Counties. It is one of the most common salamanders of the region and may be found in nearly all creeks and springs.

Plethodon cinereus (Green)—Red-backed Salamander. Although not common, this small salamander has been taken on several occasions in the forest where it hides under logs and loose bark.

Plethodon glutinosus (Green)—Slimy Salamander. This is one of the most common species of salamander throughout the state. In the Duke Forest it is by far the most abundant of the land salamanders. Although it has been found in pine stands, it is much more abundant in the hardwoods where it lives in and under rotting logs.

Hemidactylium scutatum (Schlegel)—Four-toed Salamander. This species is new to the records of North Carolina and, so far, has been found only in Durham County. The first specimen was taken November 3, 1933, by Dr. A. S. Pearse under a log in the forest near a small creek and was sent to Mrs. Helen T. Gaige of the Museum of Zoology, University of Michigan, for identification.

Bufo fowleri Hinckley—Fowler's Toad. This is the common toad of the North Carolina Piedmont. It is very abundant from April through September.

Bufo americanus americanus (Holbrook)—American Toad. It is possible that there is no justification for listing this species as occurring in the Duke Forest. However, occasionally specimens are taken that fit the description of *B. americanus* more closely than *B. fowleri*. Burt (1938) reports finding *B. americanus* in Wayne County in the North Carolina Coastal plain. If his record is correct, probably the species occurs in Durham and Orange Counties. The American toad is abundant in the mountain regions of North Carolina.

Acris crepitans Baird—This is a common species wherever there is water. Specimens have been taken at all seasons of the year, even in mid-winter when the weather is mild.

Pseudacris nigrita feriarum (Baird)—Eastern Chorus Frog. Of the five species of Pseudacris known to occur in North Carolina this is the only one found in the Piedmont region. It is a very common species during the winter and spring months, but is seldom seen in summer. Males often begin calling as early as November and continue as late as May. They are particularly vociferous in the afternoon and at night in warm damp weather from January through March. Breeding takes place in almost any little puddle, in swampy areas, or along the edges of streams.

Hyla versicolor versicolor (LeConte)—Tree Toad. The common tree toad occurs abundantly throughout North Carolina. It is very common during the summer months when it may be heard calling from shrubs and trees in the vicinity of ponds.

Hyla crucifer Wied—Spring Peeper. This is the second frog to begin calling in spring; it is preceded only by the chorus frog. Weather permitting, males are usually heard by mid-February.

Rana catesbeiana Shaw—Bullfrog. The bullfrog frequents the larger,

permanent bodies of water. Ideal habitats for this water-dwelling species are not numerous; consequently it is not as abundant as perhaps it otherwise would be.

Rana clamitans Latreille—GREEN FROG. The green frog is much more abundant than the bull frog. It is found near springs, in small wooded creeks, ponds, swampy areas, along the banks of rivers; in fact, almost any place where there is permanent water.

Rana sphenocephala (Cope)—SOUTHERN LEOPARD FROG. This is the most common of the three grass frogs to be found in the Piedmont region. It is probably second only to the green frog in abundance. Eggs are laid in March and early April.

Rana palustris LeConte—PICKEREL FROG. This is not a common frog but specimens are taken occasionally. Both this species and the preceding appear to prefer ponds, but are frequently taken along wooded creeks.

Rana pipiens Schreber—NORTHERN LEOPARD FROG. While the great majority of the grass frogs of the North Carolina Piedmont are easily distinguished as *Rana sphenocephala*, occasionally specimens are taken that grade into *R. pipiens*. The difficulty that sometimes arises in separating these two variants lends support to the contention of Burt (1938) and others that there is doubt as to the validity of recognizing *R. pipiens* and *R. sphenocephala* as full species. However, until this group of frogs has been restudied both species must be considered to exist in the Duke Forest.

Gastrophyne carolinensis (Holbrook) — SMALL-MOUTHED TOAD. This species is often found under logs in the forest and may be heard calling from the neighborhood of ponds and swampy areas throughout the summer months. It is not as abundant in the Piedmont region as in the coastal plain.

Reptilia

Sceloporus undulatus undulatus (Latreille)—FENCE LIZARD. This is the most abundant of North Carolina lizards and ranges throughout the state. It is very common in both pine and hardwood stands.

Eumeces fasciatus (Linné) — BLUE-TAILED SKINK. This is a common species in the hardwood stands. Eggs, with an attending female, are often found under the loose bark of rotting logs in late June and in July.

Cnemidophorus sexlineatus (Linné) — SIX-LINED RACE-RUNNER. This lizard lives in the open more than do the two preceding species. It frequents the borders of plowed fields and other open spaces in the forest and is often seen crossing highways.

Leiolopisma unicolor (Harlan)—GROUND LIZARD. This small secretive species is common in the hardwood stands, scampering through the leaf litter and hiding under logs.

Ophisaurus ventralis (Linné)—GLASS SNAKE. Although not rare this legless lizard is seldom seen. Several excellent specimens have been taken. Appar-

ently it is more abundant in the coastal plain than in the Piedmont region.

Phrynosoma cornutum (Harlan)—HORNED TOAD. This species is included as there is a possibility that it is establishing itself in North Carolina. Three wild specimens have been taken from the vicinity of the city of Durham. In June, 1932, one of our graduate students came upon some small boys in the act of killing one with stones. Upon investigation it was learned that about two years before a dozen horned toads brought from Texas had escaped from a woman living in the neighborhood. In the spring of 1935 another graduate student captured a specimen in a plowed field about five miles from where the first specimen was taken. On July 9, 1940, a third specimen, a female, was found by a workman while removing a pile of rubbish. This was on the outskirts of the city several miles from where either of the other two were found. On July 21 this specimen laid twenty-four eggs in the laboratory. When found all but three of the eggs had been badly mangled by the lizard in attempts to get out of her cage. One of the surviving eggs was opened a few days later and found to be fertile. The lizard died in early August during unusually hot weather and the two remaining eggs failed to hatch. There is no way of knowing if all three specimens of horned toad were from the same batch that escaped ten years ago, but the potential possibility of this species establishing itself in North Carolina cannot be dismissed. However, there should be more records of its presence before it is officially added to the fauna of North Carolina.

Carphophis amoena amoena (Say)—WORM SNAKE. This small snake is fairly common in the hardwood areas.

Diadophis punctatus punctatus (Linné)—RING-NECK SNAKE. This is another fairly abundant snake found in and under rotting hardwood logs. Eggs and adults of the ring-neck snake have been taken in the same log with eggs and adults of the preceding species.

Storeria dekayi (Holbrook)—DEKAY'S SNAKE. This is a common snake in the hardwood stands of the forest. It is also frequently found under boards and logs in the neighborhood of dwellings.

Storeria occipitomaculata (Storer)—RED-BELLIED SNAKE. This species of Storeria is perhaps more abundant than DeKay's snake. Many specimens have been brought in by children who are captivated by the bright color of the belly.

Cemophora coccinea (Blumenbach)—SCARLET SNAKE. This species seems to be relatively rare. The few specimens that have been taken were found in hardwood stands.

Haldea valeriae valeriae (Baird and Girard)—VALERIA'S SNAKE. This is not a common species. Only a few specimens have been taken.

Haldea striatula (Linné)—GROUND SNAKE. Of the two species of Haldea this is by far the more common. It is usually found under logs in the forest or rubbish piles near dwellings.

Heterodon contortrix (Linné)—PUFFING ADDER. This is a common snake throughout North Carolina. It frequents the more open spaces and has been taken in dirt roads, open fields, and meadows.

Opheodrys aestivus (Linné)—ROUGH GREEN SNAKE. This snake is commonly found in meadows and other open grass lands where it hunts insects. Specimens have also been found among the foliage of shrubs and low growing trees. It is seldom seen in heavily wooded areas.

Coluber constrictor constrictor (Linné)—BLACK SNAKE. This common species seems to prefer the dried and more open parts of the forest. It has been taken in open fields, clearings, and in wooded areas where the undergrowth is not too thick. It seems to avoid the damp bottom lands that are covered with dense vegetation.

Elaphe obsoleta obsoleta (Say)—PILOT BLACK SNAKE. This is the largest and one of the most common of the snakes of the forest. It doesn't hesitate to live near human habitations and is well known to the farmers.

Lampropeltis getulus getulus (Linné)—COMMON KING SNAKE. This is the most abundant of the three king snakes in the forest. It is found in both pine and hardwood stands, in clearings, and on farm land.

Lampropeltis rhombomaculata (Holbrook) — BROWN KING SNAKE. Although not common this nake has been frequently found crossing highways and wooded roads. Farmers sometimes mistake it for the copperhead.

Lampropeltis elapsoides elapsoides (Holbrook)—RED KING SNAKE. Judging by the few specimens taken this is a relatively rare species in the forest.

Thamnophis sauritus sauritus (Linné)—RIBBON SNAKE. This species is frequently found along streams, but is not as abundant as its relative, the common garter snake.

Thamnophis sirtalis sirtalis (Linné)—GARTER SNAKE. This is a common species and is usually one of the first to be seen in the spring. Most specimens have been taken not far from water. They have often been found in dry creek beds under stones.

Natrix septemvittata (Say)—QUEEN SNAKE. This water snake can usually be found in shallow places in the larger streams where the water flows rather rapidly over stones. It is very common in New Hope Creek.

Natrix sipedon sipedon (Linné)—NORTHERN WATER SNAKE. Although found near and in ponds and streams this common water snake apparently does not seek as fast-flowing water as does the queen snake. Locally it is known as the "water moccasin"; consequently it is thought to be poisonous and many are therefore killed each year.

Agkistrodon mokasen mokasen (Beauvois)—COPPERHEAD. This is the only poisonous snake definitely known to occur in the forest. It is fairly common in hardwood stands and several have been taken in bottom lands.

Crotalus horridus atricaudatus (Latreille)—CANEBRAKE RATTLESNAKE. It is extremely doubtful if the canebrake rattler occurs in the Duke Forest, but it is mentioned because its presence in this region has been reported in the older literature. No specimens have been taken in either Durham or Orange Counties

for a great many years. Brimley (1917), in speaking of changes in the vertebrate fauna of North Carolina, says, ". . . the banded rattlesnake *(Crotalus horridus)*, although once ranging throughout the State is now confined to the mountainous region of the west and the coastal swamps. . . ." Brimley probably refers to both *C. h. horridus* (timber rattler) and *C. h. atricaudatus* (canebrake rattler). It is the latter subspecies that was once a resident of the Duke Forest and vicinity and is now confined to the coastal region.

Terrapene carolina (Linné)—Box Turtle. This is by far the most abundant turtle in the Piedmont region of North Carolina. Many specimens are taken in hardwood stands and along highways. Young box turtles are sometimes found in aquatic habitats.

Kinosternon subrubrum subrubrum (Lacépède) — Mud Turtle. This turtle ranks second in abundance in the forest. It is common near and in streams, especially sandy creeks.

Stenotherus odoratus (Latreille)—Musk Turtle. This species has been found only rarely. The few specimens taken were in creek beds.

Chrysemys picta picta (Schneider) — Painted Turtle. Although not abundant, painted turtles may usually be found in ponds and larger streams, such as New Hope Creek.

Chelydra serpentina (Linné)—Common Snapper. A few specimens have been taken from swampy areas, sluggish streams, and stream cut-offs.

Pseudemys concinna concinna (LeConte)—River Terrapin. This large turtle lives in the rivers. It is quite common in the Eno River where specimens are frequently seen on the rocks in mid-stream.

Summary

An annotated list of the fifty-four species of amphibians and reptiles collected over a ten-year period in the Duke Forest is given. This is essentially a record of the herpetological fauna of the North Central Piedmont region of North Carolina.

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Habit and Habitat Studies of the Massasauga Rattlesnake (Sistrurus catenatus catenatus Raf.) in Northeastern Illinois*

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Introduction

Although it has been known for a number of years that the massasauga rattlesnake (*Sistrurus c. catenatus* Raf.) inhabits the Des Plaines River valley in the northern part of Cook County and the southern part of Lake County in Illinois, no studies have been published concerning the habits or habitat of this aggregation. In fact, no attention was directed towards the colony outside of that of a few collectors who were familiar with the area until the summer of 1933 when several rattlesnakes appeared in a picnic ground of the Forest Preserve of Cook County.

The mere indication of rattlesnakes in areas used for public recreation instigated an investigation of all lands adjoining the Forest Preserve property. Although local reports placed the annual kill in the neighborhood of one hundred snakes, a check up revealed that snakes killed or collected by local people in Cook County numbered closer to a dozen than one hundred.

In the summer of 1937, the Forest Preserve District of Cook County placed an investigator in the area for a period of approximately two months. During this period eleven adult snakes were collected.

During the years 1937 and 1938 from the time the snakes emerged from hibernation until they returned, the author collected in the southern portion of Lake County on the Des Plaines River floodplain (Fig. 1).

Collecting was carried on most intensively in the spring following emergence from hibernation. During this period there is a concentration of snakes in the area on the east side of the floodplain forest. It is probably in this area that mating occurs. During the two years the author collected a total of twenty-six adult snakes.

Inasmuch as these snakes confine themselves to relatively unfrequented areas, they present only a very slight problem as far as human welfare is concerned. From all indications the population has decreased considerably as has the area within which the reptiles are found. This opinion has been confirmed by collectors and local landholders who report that only a few rattlesnakes have been observed or killed recently. In one instance it was reported that where eight snakes had been killed or captured in 1937, only three yearlings

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were taken in 1938. This apparent decrease in population is due to several factors: in the first place, the construction of a bridge across the river on Deerfield Road destroyed many snakes hibernating in the rocky crevices near the river; the subsequent increase in motor traffic along this road has been an important factor in the decrease of rattlesnake population; collection of gravid females has greatly reduced the number of young born in the region; and finally, organized killings, which include the turning out of pigs into the fields adjoining the forest, have been a potential factor.

In consideration of these factors, none of which are natural, a few years' time may see the total extermination of a comparatively inoffensive reptile which, before the advent of the white man, was quite commonly distributed over the prairies of this state (cf. Cope, 1900).

General Distribution and Habitat

Distribution.—Although the range of the massasauga is greatest in the grassland biome, yet a large part extends into the deciduous forest regions as far east as the state of New York (See Fig. 2). Atkinson and Netting (1927) have offered as an explanation of this eastward extension of the range the possibility of a prairie stage in Ohio and Pennsylvania antecedent to the deciduous forest biome which now exists. Schmidt (1938) correlates the range of the massasauga with the postglacial eastward extension of the grassland in North America, stating that the range of the snake is local in its eastward part, being confined to the region of sphagnum bogs; however, in the region north of St. Louis it is decidedly a prairie animal. In the study of this snake, the author has found that in northeastern Illinois the habitat is marsh and swampland.

Guthrie (1926) states that since the intervention of man, the massasauga

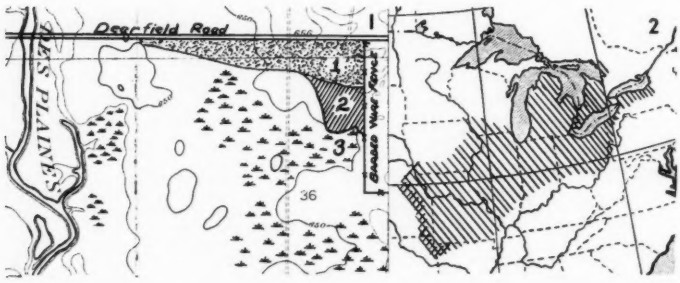

Fig. 1. Map of the area in which study of he Massasauga Rattlesnake *(Sistrurus c. catenatus)* was made. The stations at which the studies were made are numbered: (1) Oak-Elm Associes; (2) Dogwood-Hawthorn Associes and Blue Grass-Hawthorn Associes; (3) Cattail-Sedge Associes.

Fig. 2. Range of *Sistrurus catenatus catenatus*. (from Klauber, 1936b). Cross-hatching indicates intergradation with *S. c. tergeminus*.

has become less abundant in the prairies of Iowa than formerly and is probably found in the greatest numbers where the country is swampy. This viewpoint is entertained also by Noble (in Fisher, *et al.*, 1927), Thompson and Gaige (1928), and Cope (1900).

Actual distribution and frequency records for the entire range of this snake are few and in many cases inaccurate; consequently, Fig. 2, which is copied largely from Klauber (1936b) is more or less general.

The available records for Illinois fall within Klauber's map and indicate that the range of this snake extended over the greater part of the state, reaching southward to the vicinity of the Ozark foothills.

Garman (1892) states that the massasauga was common throughout the state. He cites records from Cook County, Galesburg, Peoria, Pekin, Normal, and Farmer City. All these records except the one from Cook County lie within the area covered by the eastward extension of the grassland biome. The records within the past decade are primarily from swampy or poorly drained forest edge.

As has been mentioned in the introduction, the local distribution in northeastern Illinois is limited to the floodplain of the Des Plaines River in the southern part of Lake County and the northern part of Cook County. The range extends northward into Lake County for a distance of about one mile and southward into Cook County as far as the town of Des Plaines. One report has been called to the author's attention of a rattlesnake being taken ten miles south of Des Plaines, but the authenticity of this identification is doubtful. The point of concentration of the snake is in the area studied (Fig. 1).

In this region the rattlesnakes, in general, confine themselves to the east bank of the river and the adjoining floodplain. They rarely occur on the west bank of the river.

General Habitat.—Following the period of the glacier, there was an eastward extension in the range of a number of western prairie animals into the open areas left by the glacier. Thus it was that prior to settlement by white men, the massasauga ranged over most of the prairie regions from Ohio west into Iowa (cf. Garman, 1892; Conant, 1938; Cope, 1900).

However, as the white man immigrated westward, the lands were cleared for cultivation and the swamp areas of Pennsylvania, Ohio, Indiana, Illinois and other states were drained to provide land for an increasing population. Atkinson and Netting (1927) state that as early as 1866 the massasauga began to disappear from the swamps following the drainage activities. Hay (1893) described the condition in Illinois:

> On the prairies of Illinois before the country became thickly populated, these reptiles were extremely abundant, and the killing of two or three dozen of them in a season was not an unusual thing for any farmer's boy. Now in this same region not one is to be seen in years, this disappearance of these snakes has been supposed to be due to destruction wrought among them by hogs. Yet on those prairies in those days there were no roaming hogs. The extinction of the snakes may be due to the breaking up of the soil, the drainage of the ponds, and the clearing away of rank vegetation, which

furnishes them protection. At the present day it is only in the swamps and marshes that they are found.

Hay's account may be taken as a general statement for the status of this species throughout its present range. At the present time it is never found far from the protection of rank vegetation and the thick cover of marsh and swamp regions. This fact is borne out by habitat observations of numerous writers.[1]

Description of the Area in Northern Illinois

The east bank of the Des Plaines River from Wheeling to Deerfield, Illinois, is forested for a distance of from one quarter to a half a mile in width. It is on the forest edge adjoining the Vernon Ridge Country Club that the most intensive study was made.

A barbed wire fence extends in a north and south direction from Deerfield Road to the southern limit of the country club (Fig. 1). At the present time there is an invasion of prairie by forest along the fence. At the north end of the fence the subclimax condition has been reached (oak-elm) so that early and late seral stages are mixed together. About one quarter of a mile south of Deerfield Road the associes are more defined. This particular area is flooded during the spring and fall. Marsh areas are also common as can be seen from Fig. 4. It is in these wet places that the rattlesnakes are most commonly found during the months of May and June. However, no specimens have been taken from areas where there was standing water.

In describing the various stations which were studied, each is considered as an associes, or developmental stage, of the oak-hickory climax.

1. *Typha latifolia-Carex* sp.-*Rana pipiens* Associes.—This associes is covered by water the greater part of the year and even in the hottest part of the summer the ground is quite moist. The cattail (*Typha latifolia* L.) and the sedge (*Carex* sp.) are the dominant plants. Other plants found in the locality are subdominant to the cattail and the sedge. Among the common subdominants are the swamp milkweed (*Asclepias incarnata* L.) and manna grass (*Glyceria* sp.), which are near the edge of the associes, and blue grass (*Poa compressa* L.) which is found at its outer edge.

Although the rattlesnakes have been taken from under cover in the wet places near the border of this associes, in my own collecting and from the data of other collectors, there have been no snakes taken from places where there was standing water.

2. *Cornus florida-Crataegus mollis-Poa compressa* Associes.—This associes represents the earliest stage of the floodplain forest sere. It lies in an ecotone between the prairie and the forest and contains plants which are characteristic of both. The flowering dogwood (*Cornus florida* Walt.) and the hawthorne (*Crataegus mollis* (T. & G.) Scheele) are the dominants although they are

1 Branson (1904) working in Kansas, Breckenridge (1938) in Minnesota, Ditmars (1936), Guthrie (1926) in Iowa, Hurter (1911) in Missouri, Pope and Dickinson (1928) in Wisconsin, Reddick (1896) in Indiana, Wright (1919) in New York, and Ruthven and Gaige (1928) in Michigan.

little more than shrubs. The blue grass is the common plant in the herb layer socies and definitely holds a dominant position. A number of other plants occur as subdominants and influents. The area covered by this associes is flooded in the spring, but generally all the surface water has receded by the latter part of April or early May. The soil remains moist through the greater part of the summer although the surface may become dry.

Rattlesnakes are found quite frequently in this associes and have been collected in the open and from under cover. In cases where the snake was caught in the open, the collecting was done in the early morning or evening. This fact tends to bear out the theory that the massasauga is crepuscular in its activity under natural conditions.

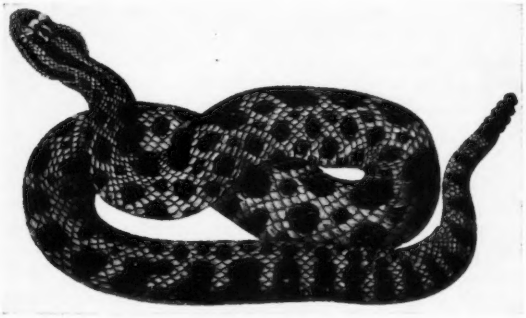

Fig. 3. *Sistrurus catenatus*, after Bocourt.

3. *Poa pratensis-Crataegus mollis-Sistrurus c. catenatus* Associes. — The habitat in which the majority of specimens were caught is a black mixed loam (cf. Hopkins, *et al.*, 1915). Inasmuch as the area was probably a pastured woodlot at one time, a number of plants characteristic of disturbed areas occur; and numerous hummocks, which are common in black mixed loam, are present. The dominant trees in the ecotone are hawthorne and green ash (*Fraxinus lanceolata* (Bork.) Sarg.). Among the dominant herb-like plants are blue grass, sedge, and wild rye (*Elymus* sp.). Other plants collected in this area are subdominant to the above mentioned plants.

It is in this area that the majority of rattlesnakes have been captured. The ground is wet during early spring and summer, and natural and artificial cover is plentiful. In the spring before the snakes spread out into the swamp region, there may be several individuals occupying the same piece of cover.

4. *Quercus macrocarpa-Populus deltoides-Sciurus niger rufiventer* Associes. --This associes is situated on higher ground than the previously mentioned associes and consequently is flooded only a very short time of the year. It is probably an older section of a pastured woodlot; this fact is indicated by the

blue grass, wild strawberry (*Fragaria virginiana* Duchesne), and the beggar's tick (*Bidens cernua* L.) as well as a number of grassy hummocks.

The forest edge has been restrained by close cutting of vegetation along the barbed wire fence and is consequently mixed with later seral stages of the floodplain forest. The subclimax trees of burr oak (*Quercus macrocarpa* Michx.) and American elm (*Ulmus americana* L.) are the dominants. The understory trees such as poplar (*Populus deltoides* Marsh.), sumac (*Rhus canadensis* Marsh.), and a few green ashes are subdominants. In the shrub layer occur such plants as the hazelnut (*Corylus americana* Walt.), dogwood and currant (*Ribes vulgare* Lam.). In the herb layer socies is found the blue grass, wild strawberry, beggar's tick, goldenrod (*Solidago canadensis* L.) and ragweed (*Ambrosia artemisiifolia* L.).

No aggregations of snakes have ever been found in this forested area. However, on several occasions individual snakes have been captured in this associes. It is quite possible that the specimens caught were migrating because in each case the snakes were moving about, and in no case was a snake taken from under cover in the forested area although there was an abundance of natural shelter.

Life History

The Adult.—The massasauga attains adulthood or sexual maturity during its third year of life and, at this time, is about three times as long as it was at birth. In separating adults from juveniles, it was found that in the collections of 1938 there were no specimens obtained between the lengths of 42 cm. and 54 cm. Inasmuch as the 42 cm. specimens were known to be yearlings and since a specimen 54 cm. in length gave birth to young, the arbitrary length for adults was taken at 54 cm. or larger.

During the late spring and early summer of 1937 and 1938 twenty-six adult specimens were collected in the area. The largest measured 73.1 cm. total length and the smallest adult measured 54.1 cm. total length. These specimens taken together with a number of others which had been collected from the same area had an average length of 63.7 cm. It was found that the average length for males was slightly greater than that for females.

In adult specimens in which the sex had been determined, the ratio of the length of the tail to the total length of the body was 10.9 per cent in the males and 8.3 per cent in the females.

Klauber (1936a) in determining the sex ratios among various species of rattlesnakes observed that in a group of 113 massasaugas there were 57 males and 56 females, or a M/F ratio of 1.04. Since he believes that the sexes are born in equal numbers he presents several possible explanations for higher ratios which he got with other rattlesnakes which he studied. He suggests that there may be a higher mortality among females than males. He also states that the males are more active than the females during the summer and early autumn and are more likely to be caught than the females which, heavy with young, tend to remain under cover.

Mating and Birth of the Young.—Klauber (1936a) working with *Crotalus viridis oreganus* (Holb.) and *Crotalus ruber* (Cope) observed that females go into the third hibernation (an age of about twenty-six months) carrying developing ova. These ova increase about six per cent in width and length during the hibernation period. In the following spring the ova are fertilized and the brood hatches about the time that the mother completes her third year of life.

In the area in northeastern Illinois copulation occurs in late April, May, or even June in years where a late spring has occurred. The best account of the

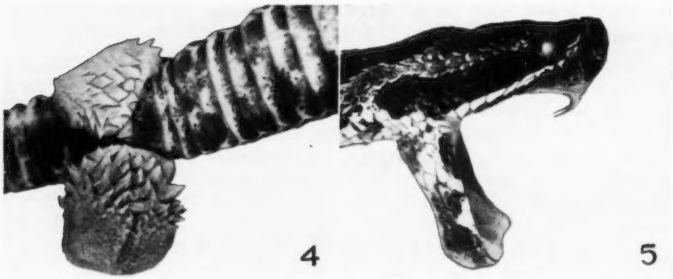

Fig. 4. Hemipenes of adult male showing bifurcation of each hemipenis.
Fig. 5. Head of adult massasauga. Note that there are two fully developed fangs on the right side.

courtship is given by Guthrie (1927) who observed a pair of massasaugas in captivity:

> On May 7th at three different times the male, which measured about twenty-nine inches, was seen trying to mate with the female which was about three inches longer. She seemed entirely passive. The tail of the male was wrapped around the other with the vents near together but not in contact. The male showed a sort of spasmodic twitching, mainly of the posterior half, but sometimes of the entire body. At one time his head exhibited excitement, the tongue frequently darting far out and the head being thrust about above the head of the female who paid not the slightest attention.

The copulatory organs of the male consist of two hemipenes which normally lie on either side of the mid-line at the base of the tail (Fig. 4). When they are in use they are evaginated, the inner surface becoming the outer. Each hemipenis is bifurcated and armed with a number of short retracting spines. During the act of copulation one of the hemipenes is introduced into the cloacal opening of the female.

Guthrie *(loc. cit.)* states that on Oct. 31st and Nov. 1st the female discharged thirteen undeveloped eggs as a result of an unsuccessful mating. There is also a possibility that the eggs are reabsorbed in cases where fertilization does not take place. This fact is indicated in the case of one female taken in the area studied in northeastern Illinois. This snake was taken on July 12 and contained a number of eggs which ranged in size from 3 mm. to 13 mm.

Two females taken from this same region during the middle of May later gave birth to young. Copulation must have occurred shortly before capture since there was not possibility of mating while the snakes were in captivity. Atkinson and Netting (1927) conclude from their observations that mating occurs in late April or early May.

From observations and collecting in northeastern Illinois and from the evidence presented by previously mentioned writers, the author believes that the gestation period is usually fifteen or sixteen weeks.

During the late spring of 1937 six gravid females were collected from the area. These snakes were placed in an 'L'-shaped cage which permitted them exposure to the sun on the south and west sides.

The dates on which the births occurred were Aug. 17th, 20th, 30th, 31st, and in two cases on Sept. 1st. In each case the female gave birth to the young during the day between the hours of 6:30 A.M. and 4:15 P.M. In the case of one litter of eight massasaugas, all of them were born within one hour, averaging one extrusion per every seven and one half minutes. It is interesting to note that Gloyd (1934) working with copperheads observed that birth of the young occurred during the night.

TABLE 1.—Measurements of Six Litters Born in 1937

Date	Length of female	No. in litter	Average length	Range of length	Undeveloped embryos
August 20	55.1 cm.	8	20.4 cm.	19.0-23.1 cm.	none
September 1	65.4 cm.	14	23.2 cm.	20.6-24.9 cm.	none
September 1	66.5 cm.	5	22.5 cm.	20.6-24.1 cm.	3
August 31	67.1 cm.	8	25.0 cm.	22.9-26.4 cm.	11
August 30	61.7 cm.	12	20.5 cm.	19.0-21.6 cm.	1
August 17	unknown	10	22.9 cm.	unknown	unknown

Atkinson and Netting (1927) found from observations made of females that five to nine young are produced in late July and early August. Hay (1887) records the birth of two broods of five and six young respectively about Sept. 1st which measured three to four inches in length. Werner (Brehm, 1912) states that during early September about six young were born. Since much of his material concerning massasaugas is derived from the accounts of Hay, it is quite possible that he is referring to Hay (1887). The date of birth and the number of young given by Atkinson and Netting (1927) and Hay (1887) differ greatly from the author's records taken in northeastern Illinois. The size of the young which Hay records are from $1/3$ to $1/2$ the size of the young obtained in Illinois broods.

The records of Swanson (1933) and the recent account of Conant (1938) agree quite closely with the data obtained in northeastern Illinois. Unfortunately only one of the gravid females listed by Swanson actually gave birth to young although all the others contained young approximating the size of the litter which was born. The results of Swanson's records from western Pennsylvania are given in tabulated form to facilitate comparison with Table 1 (See Table 2).

TABLE 2.—Measurements of Four Litters Collected by Swanson (1933).

Date	Length of female	Average length	Range of length	Total number	Undeveloped embryos
August 17*	59.4 cm.	20.7 cm.	20.0-21.9 cm.	8	5
August 21*	59.7 cm.	14.0 cm.	13.5-14.6 cm.**	8	..
September 7	66.0 cm.	21.7 cm.	21.1-22.2 cm.	8	one stillborn
August 24	54.6 cm.	21.6 cm.	not given***	5	..

* Snake killed or died on date given; young unborn.

** Based upon three specimens which were measured.

*** Snakes found with female; only one measured.

The account of Brehm (1879) quotes Geyer as having found rattlesnake eggs under a rock in Missouri. These eggs, according to Geyer, were partially buried in the soil and were about the size of pigeon's eggs. Either Geyer mistook the embryonic membranes for the egg shell or else the eggs were those of some oviparous snake. It is interesting, however, that at this early date Geyer regarded with suspicion the belief that young snakes take shelter in the mouth of the mother.

In discussing the mortality of juveniles, Klauber (1936a) bases the high mortality on the fact that the young are more careless in their concealment than the adult and are preyed upon by animals which could not successfully cope with an adult.

Another factor which the author believes enters into the mortality of the new born snakes is the inability to find food. Although the young live for a while on the remaining contents of the yolk sac (which is drawn into the body shortly after birth), they soon starve to death if they cannot find food which they can swallow. Cold winters also account for the death of some due to the fact that the young may not hibernate at a sufficient depth.

Growth.—The growth curve for the rattlesnakes is quite steep for the first three years but levels off thereafter. Klauber (1936a) states that at the age of one year *Crotalus viridis oreganus* has doubled the length at birth and at three years of age is three time the length at birth.

The writer has found that the average length of the new born massasaugas was 23.3 cm. The yearlings averaged 37.5 cm., which is an increase of about 65 per cent. The smallest adult (age three years) was 54.1 cm. in length or two and one half times the average length for new born snakes.

Naturally a number of factors influence the rate of growth, food being one of the greatest, but judging from the rodent population and the amount of cover, there is little danger that the maximum carrying capacity of the area in northeastern Illinois will be reached within the next few years.

In connection with growth the question arises as to whether or not there is a point in the life history of reptiles at which growth ceases. The oldest specimen in the author's collection was taken at an age of four or five years.

During the two years which this snake was in captivity it continued to grow; however, the growth was quite slow. In this case at least, growth continued after the snake had reached maturity.

Another question concerning growth is whether or not a stunted individual can reach normal adult size. Where stunting has been due to poor environment (lack of sunshine, low temperature, lack of food, etc.), normal growth can frequently be obtained if the conditions are remedied. In the case of several massasaugas which had grown only slightly more than one inch during the first year, it was found that more food under warmer conditions caused an increase in growth slightly better than that of snakes in natural conditions.

Food and Feeding Habits.—With the exception of breeding activities, the feeding habits of this snake have been the most neglected aspect of its life history inasmuch as many of the observations have been made from captive snakes and few stomach examinations have been made.

Stejneger (1893) states that mice and other rodents were found in the stomachs of massasaugas, and Ruthven (1911) relates finding a frog in the stomach of a massasauga, snake remains in the stomach of two others, and the dried remains of a massasauga in the stomach of another. This record is particularly valuable inasmuch as it proves that the massasauga will not only eat cold-blooded vertebrates but that it may eat them after they have been dead for some time. Ruthven, Thompson and Gaige (1927) report that stomachs examined contained mice and similar animals. Guthrie (1926) and Conant (1938) likewise list rodents as being the principal item of food.

Several writers other than Ruthven have pointed out that the massasauga will eat cold-blooded vertebrates. Atkinson and Netting (1927) report the eating of half-grown frogs *(Rana pipiens)* by captive rattlers. Curran (1935) states that captive massasaugas ate frogs, refusing all else. Ditmars (1936) also includes frogs in the diet of this snake.

In examining specimens in the Illinois Natural History Survey collection the author fortunately chanced upon a specimen collected at Pekin, Illinois, in 1873. Inasmuch as there was a conspicuous bulge in the mid-portion of the body, a dissection was made which revealed a perfectly preserved white-footed mouse *(Peromyscus leucopus noveboracensis)* which measured 8 cm. (body length). The snake itself had a total length of 31 cm. with a tail length of 3.5 cm. The snake was undoubtedly killed and preserved shortly after it had fed inasmuch as very few hairs were lost from the body of the mouse.

A stomach examination of a massasauga collected in the dunes of Indiana in 1934 revealed a field mouse (*Microtus* sp.) almost completely digested. In this case identification of the rodent was based upon the skull.

It has been the author's experience that only warm-blooded animals are eaten by captive massasaugas. In each case of feeding the snake ate either a field mouse or a white-footed mouse although cold-blooded animals were also placed in the cage. The average time for an adult massasauga to swallow an adult Microtus was about fifteen minutes. The snakes generally seek cover

after eating and remain in one place until digestion is nearly completed. The exact time required for digestion is not known; however, one captive yearling which had not fed for over a month defecated forty-one hours after swallowing a small Peromyscus. In another case fifty-six hours elapsed between the time of feeding and the first defecation. During this period the snake remained entirely under cover. In both cases the snakes were kept in a cage at 27 degrees centigrade.

Regarding the length of time that the massasauga can survive without food, very little is known except that they can survive for a number of months if provided only with water. One adult snake taken from the area studied ate for the first time in captivity after ten and one half months.

As indicated earlier, the newly born snakes subsist on the remaining contents of the yolk sac for some time after birth. This fact was observed at an early date by LeConte (1853). In the case of young born in captivity, the author found that they could be quite successfully fed on dismembered portions of mice.

The Poison of the Massasauga

There has been much controversy considering the effects of the bite of the massasauga. Werner (Brehm, 1912) quotes Kirtland as saying that the bite is not much worse than the sting of a hornet. Diametrically opposed to this viewpoint is Branson (1904) who reports the death of a five-year-old child from the bite of a massasauga. However, since neither of these cases afford very complete evidence, it is more profitable to take the accounts of recent writers who have had actual experience with the snake.

One of the most conclusive works on snake poisoning has been that of Githens (1935) who worked with a number of species of poisonous snakes in the United States. The results of his data for the massasauga are given in Table 3.

TABLE 3.

Without antivenin			With antivenin			Total			Length of snake
Total	Die	%	Total	Die	%	Total	Die	%	(average)
5	0	0	19	0	0	24	0	0	24 inches

Atkinson (Atkinson and Netting, 1927) reports being bitten on the hand. The hand became swollen and partially disabled, but no symptoms of general poisoning appeared. Treatment for the bite was cutting and suction.

In handling young snakes several months old the author was bitten on the finger. A slight throbbing was felt in the region of the wound but no other symptoms were noted.

Concerning the effect of the bite upon small mammals and other vertebrates, Swanson (1930) states that a small rattler bit a mouse which died within twenty-three minutes. In another case two adult each bit mice which died in three minutes and twelve minutes respectively. Werner (Brehm, 1912)

quoting from Selous states that a mouse died within thirty seconds after being struck by a massasauga. It has been the author's experience that a much longer time than that given by Werner is required for the poison to kill mice, the shortest period being ten minutes and the longest period being fifty minutes.

Curran and Kauffeld (1937) state that the poison is so weak that the snake has developed the habit of holding unto its prey after striking. Inasmuch as the fangs of this snake are quite short, see Fig. 5, this holding may permit the snake to imbed its fangs deeply enough to render a mortal bite.

Since experiments have shown that, drop for drop, the poison of the massasauga is as potent or more so than that of the diamond-back rattlesnake, and since the effect of the bite depends upon the condition of the snake and also the person or animal which is bitten, it is best to regard this snake with caution and respect.

Summary

1. Previous to the settlement by the white man, the massasauga was quite abundant over the prairie regions of the middle west; however, since settlement of these prairie areas the snake has been extirpated except in bogs, marshes, and unfrequented floodplains.

2. The region in which these snakes are found in northeastern Illinois is a low floodplain of the Des Plaines River. The snakes prefer the moist or wet places but are not found where there is standing water.

3. The area in which the snakes are found is an ecotone between forest and prairie. There is a rapid invasion of prairie by forest; consequently, in places where there is close cutting of vegetation there is a mixture of late and early stages.

4. The size of the adults ranges from 54.1 cm. to 73.1 cm., the average length being about 63.7 cm. The average length of the males was found to be slightly greater than that of females. The ratio of the length of the tail to total body length was found to be 10.9 per cent in the males and 8.3 per cent in the females.

5. In northeastern Illinois copulation occurs in late April or in May. In cases where the eggs are not fertilized they are probably reabsorbed by the body. The length of the period of gestation ranges from fifteen to sixteen weeks, the young being born in late August or early September.

6. The young were all born during the day and averaged one extrusion per every seven or eight minutes. Record of total numbers born and size of the young at birth do not check with early writers but agree with later workers. The number and size of the young are considerably greater than early writers supposed.

7. Inability to find food, predation and cold winters are the most important factors in reducing juvenile populations.

8. Growth is doubled during the first year and increases steadily so that by the end of the third year the snake's total length is nearly 2.5 times as great as it was at birth. It is believed that the massasauga continues to grow throughout its life span and that retarded individuals can resume normal growth if placed under proper environmental conditions.

9. Although cold-blooded animals have been mentioned as part of the diet of this snake, the author's experience has been that only warm-blooded animals were taken. The period for digestion was found to be between forty-one and fifty-six hours at a constant room temperature of 27 degrees Centigrade.

10. The bite of the massasauga according to authentic records has never been fatal. The fangs are so short and so little poison is injected into the bite that frequently the only symptoms noted in man are swelling and temporary disablement of the part which is bitten.

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The writer wishes to express his deep thanks to Dr. V. E. Shelford under whose direction the problem was done. To Dr. H. K. Gloyd of the Chicago Academy of Sciences, who placed at the writer's disposal many specimens and an extensive bibliography, a debt of thanks is felt. The writer wishes to extend his thanks to Dr. H. J. Fuller of the Botany Department of the University of Illinois for the identification of many plants. To Dr. Sarah E. Jones and Mr. E. J. Koestner the writer is grateful for many valuable criticisms and comments. The author would also like to extend his thanks to his various colleagues for their aid and many suggestions.

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A New Species of Natrix from Texas

Harold Trapido

Through the interest of Dr. A. H. Wright, the Cornell University Museum has procured a number of snakes during the past few years from Mr. Philip Harter, a most enthusiastic and energetic collector of Palo Pinto, Texas. In a miscellaneous collection received from Mr. Harter in September 1938 was a watersnake with a clear pink venter like that of *Natrix e. erythrogaster*, but with the dorsal pattern persistent as in *Natrix erythrogaster transversa*. The persistent pattern was, however, unlike that of *N. e. transversa*, or any other watersnake now recognized from North America. At the time, the snake was catalogued as an aberrant *Natrix erythrogaster*. In February, 1940, an assortment of snakes received from Mr. Harter included a watersnake identical in appearance with that which had been sent a year and a half previous. On corresponding with Mr. Harter it was possible to determine that these snakes were not occasional sports in his region, but the common and abundant watersnake in rocky habitats along the Brazos River in Palo Pinto County. Mr. Harter then supplied the writer with more than a score of specimens. These snakes were received alive, and appeared similar in color and pattern throughout a series from 9 to 32 inches in total length. It is now apparent that these represent a surprisingly distinct new species which I am pleased to name for its collector, Mr. Philip Harter.

Natrix harteri n. sp.

Diagnosis: This differs from all other North American snakes of the genus *Natrix*, excepting *N. erythrogaster*, in the presence of twenty-three scale rows and a nearly unmarked venter. From *N. e. erythrogaster* it differs in the persistence of the dorsal pattern to maturity; from both *N. e. erythrogaster* and *N. e. transversa* in the pattern of alternating dorsal spots, two scales long, alternating with lateral spots. The number of dorsal or lateral spots is fifty-eight or more, exceeding that of all the races in the related species, *N. erythrogaster* and *N. sipedon*. The dorsal pattern is uniform in intensity throughout life (see Fig. 5) while *N. e. erythrogaster* loses the pattern completely with maturity, and *N. e. transversa* has the pattern prominent with youth and obscure with age. The venter is Pale Vinaceous Pink* becoming Japan Rose under the tail, while *N. e. transversa* from the same region has the belly Pinard Yellow. The number of dorsal scale rows at midbody never exceeds twenty-three in *N. harteri* while it may reach twenty-five in *N. e. erythrogaster* (Clay, 1936) and twenty-seven in *N. e. transversa* (Clay, 1936). The head is narrow and elongate in form, rather more like *Thamnophis angustirostris* than a

* Color names which are capitalized are from Ridgway, matched with the specimens in life.

Natrix. The high number of ventrals (145 to 150) further separates *N. harteri* from the races of *N. sipedon* as presented by Clay (1938).

Holotype: U. S. National Museum No. 110927 (H. T. No. 1302), adult male, collected in rocky stretches along the Brazos River north of Palo Pinto, Palo Pinto County, Texas, early April 1940, by Philip Harter.

Description of holotype: Rostral entire, broader than high, in contact with anterior nasals, internasals, and first upper labials; internasals paired, subdeltoid, area about one-half that of prefrontals, posterior border slightly anterior to suture between posterior nasal and loreal, laterally in contact with anterior and posterior nasals, posteriorly with prefrontals; prefrontals paired, about as wide as long, combined area slightly exceeding that of frontal, narrowing laterally, broadly in contact with internasals, posterior nasals, loreal, preocular, superoculars, and frontal; frontal single, pentagonal, longer than wide, truncate anteriorly, subacute posteriorly, laterally in contact with superoculars; parietals paired, longer than wide, broadest near anterior end, gradually tapering posteriorly, laterally in contact with anterior and posterior temporals, anteriorly in contact with postoculars, superoculars, and frontal; anterior nasal about equal to posterior nasal in size, slightly higher than long, very narrowly fused above with posterior nasal, ventrally in contact with first labial only; posterior nasal slightly higher than long, ventrally in contact with first and second upper labials; loreal subquadrangular, about equal to posterior nasal in area, ventrally in contact with the second and third labials; preocular entire, much higher than long, ventrally in contact with the fourth upper labial; superocular twice as long as wide; postoculars three on the right side, two on the left, uppermost of the right side in contact posteriorly with the parietal, the lowermost in contact posteriorly with the anterior temporal, the middle one in contact posteriorly with both the parietal and anterior temporal, on the left side the upper postocular in contact with the parietal the lower with both the parietal and the anterior temporal, ventrally the lower postoculars in contact with the fifth and sixth upper labials; anterior temporal twice as long as high, subacute posteriorly, ventrally in contact with the sixth and seventh upper labials; posterior temporals two, the lower in contact with the eighth upper labial, the upper the larger; upper labials eight, portions of the fourth and fifth entering the orbit, the sixth the largest; lower labials ten, the fifth and sixth the largest, first pair in contact for part of their length between the mental and the anterior chin shield; mental triangular, about equilateral; chin shields in two pairs, each about twice as long as wide, anterior slightly longer, anterior pair in contact throughout their length, but for a small partial division by the first lower labials; posterior pair separated by three pairs of small scales; ventrals entire, 149; anal divided; subcaudals divided, 84; scale rows 23-23-23-21-19-17-17, all rows keeled, first row somewhat wider than others, dorsal scales slightly emarginate, with weak apical pores. Total length 694 mm., tail 26.5 per cent of total length (184 mm.).

Dorsum with the ground color Tawny Olive, marked with spots of Saccardo's Umber as follows: to each side of the middorsal line, spots one

or two scales wide, mostly alternating with one another and extending laterally to the sixth scale row; alternating with these are lateral spots from the first to the sixth scale row, mostly one scale wide; sixty-two such sets of spots on the body exclusive of the first somewhat enlarged blotch on the occiput. Head unmarked Saccardo's Umber, becoming paler, almost straw, on the upper labials. Venter clear, unmarked Pale Vinaceous Pink, except for the accumulation of a little dark pigment at the anterio lateral corners of the ventrals and subcaudals, particularly posteriorly; color becoming Japan Rose under the tail.

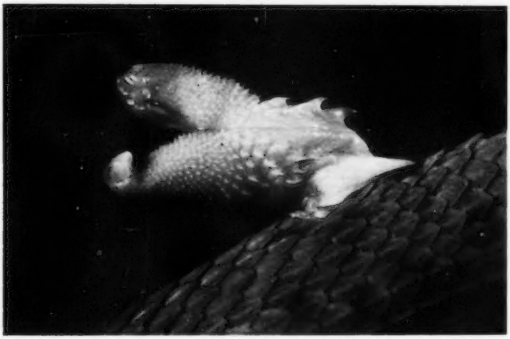


Fig. 1. Right hemipenis of the holotype of *Natrix harteri* n. sp. everted. The enlarged basal spine is five mm. in length. Also apparent are the proximal recurved spines, the distal spinules on the rami, and the nature of the sulcus spermaticus.

Penis bilobed, each hemipenis (see Fig. 1) forked, with one much enlarged basal spine five mm. in length; with lesser recurved spines to either side of the sulcus spermaticus, becoming spinules on the rami; basal portion opposite sulcus spermaticus smooth, lacking spines or spinules.

Cotypes: Cornell Univ. Museum Nos. 3100, 3101, 3103-3109, same data as the type. *Paratypes:* Cornell Univ. Museum Nos. 3110-3121 same data as the type collected in late April 1940; Cornell Univ. Mus. Nos. 3122, 2488, same data as the type, but collected September 1938.

Variation in scalation: The following review of the variation in this species is based on a study of the twenty-three cotypes and paratypes cited above.

The upper labials are eight as in the holotype with the exception of one specimen which has but seven on the right side. The lower labials are ten, with three exceptions. Two specimens have the seventh and eighth lower labials fused, thus lowering the sum of the labials to nine, while one has a split in the region of the second and third lower labials to increase the number of these scales to eleven. The number of postoculars, as may be seen in Table 1, is variable.

TABLE 1.—Numbers of postoculars in twenty-three specimens of *Natrix harteri* n. sp.

	Number of postoculars	
	2	3
Frequency on right side	17	6
Frequency on left side	15	8

Two may be taken as the "normal" number for the species as it occurs in 73.9 per cent of the snakes on the right side and 65.2 per cent on the left side. It is apparent, however, that neither one or theother of these numbers is of particular significance in the characterization of the species.

The posterior temporals are likewise variable as is shown in Table 2.

TABLE 2.—Numbers of posterior temporals in twenty-three specimens of *Natrix harteri* n. sp.

	Number of posterior temporals				
	1	2	3	4	5
Frequency on right side	1	9	11	2	0
Frequency on left side	1	8	12	1	1

Three is the most frequent number of posterior temporals occurring in 47.8 per cent and 52.1 per cent of the specimens on the right and left sides respectively.

The plates of the head, other than those reviewed above, are constant.

The ventrals vary from 145 to 150, with the mean 148. The frequency of their occurrence is shown in the accompanying histogram (Fig. 2). It is apparent that there is no evident sexual dimorphism. The subcaudals, on the other hand, show much greater variation, and correlation with sex, as may be seen in the histogram of figure three. The subcaudals in females are 71 to 76, in males 81 to 86.

The dorsal scale rows in this series of specimens were counted on the neck close behind the head, just anterior to the anus, and at five other points equidistant from each other and from the first two mentioned points: In Table 3 these counts are arranged from neck to anus, showing the extremes and average for the group.

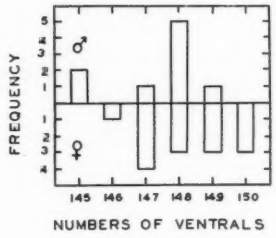
TABLE 3.—Numbers of dorsal scale rows in twenty-three specimens of *Natrix harteri* n. sp.

	Position on body						
	Neck						anus
Extremes	21-26	21-23	21-23	20-23	19-23	17-19	16-17
Average	23.26	21.60	22.75	21.12	20.33	18.16	16.29

With the exception of the counts just behind the head, which are high due to the broadening there, the highest number of rows on the body is twenty-three. Clay (1936) found *N. e. erythrogaster* to have counts as high as twenty-five at midbody, and *N. e. transversa* as high as twenty-seven. *N. harteri* has apparently fewer scale rows than *N. erythrogaster*.

Variation in proportions: The ratio of the total length to that of the tail is expressive of sexual dimorphism. The females have the tail 22.0 per cent to 25.8 per cent of the total length, while the males have the tail 25.7 per cent to 27.6 per cent of the total length.

Variation in coloration: The remarkably constant color pattern is a most striking feature of *N. harteri* of all sizes. The coloration of all the specimens seen by the writer is as described for the type above. Snakes about to shed have the color pattern somewhat obscured, as in other watersnakes, but the dorsal spots may always be easily made out by submerging the specimen in water. The number of dorsal spots on the body is a significant expression of the distinctness of this species. Clay (1936) in a study of 2446 specimens of *N. sipedon* and *N. erythrogaster* found the highest number of spots in *N. e. transversa* (31-45) and *N. s. sipedon* (28-45). *N. harteri* stands apart from these, probably the most closely related species, with counts of 58 to 65 (see Table 4).



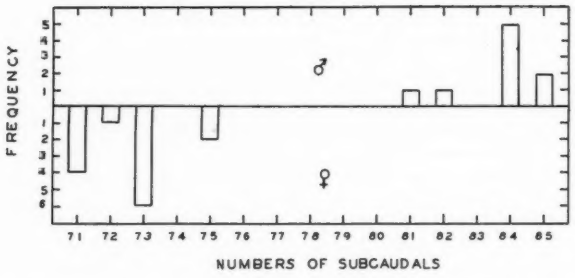


Fig. 2. Variation in number of ventrals in twenty-three specimens of *Natrix harteri* n. sp. The males are plotted above the abscissa, the females below.

Fig. 3. Variation in numbers of subcaudals in twenty-three specimens of *Natrix harteri* n. sp. The males are plotted above the abscissa, the females below. There is a striking sexual dimorphism.

TABLE 4.—Numbers of dorsal body spots in 22* specimens of *Natrix harteri* n. sp.

	Number of spots							
	58	59	60	61	62	63	64	65
Frequency	6	3	7	0	3	1	1	1

Habitat: For information on the habitat of *N. harteri*, I am indebted to Mr. Philip Harter and Miss Catherine D. Hemphill. This snake is captured along the Brazos River either under rocks along the edge, or under rocks in water less than ankle deep (see Fig. 4). Occasionally a snake is seen in the open water or when surprised on the bank, will swim across the river to the opposite shore. One specimen was caught on a log in a large pile of driftwood.

Fig. 4. Habitat of *Natrix harteri* n. sp. along the Brazos River at the type locality north of Palo Pinto, Texas. Specimens have been taken under rocks along the bank at the right and among stones in the river bed at the left. Photograph by Catherine D. Hemphill.

N. harteri is only found along the Brazos River where the bed is covered with rocks, or on the rocky portions of the banks. It has not been found on sandy stretches of the river. This species has been taken along the river at the mouth of Elm Creek, at a second rocky place along the river about one-half mile west near the bridge between Palo Pinto and Graford, and at a third locality, Chick Bend, about three miles upstream from the bridge.** This habitat is quite different from that of the other two local watersnakes, *N. e. transversa* and *N. r. rhombifera*. These are found along the creeks which are tributary to the Brazos, such as Elm Creek and Little Keechi Creek, where *N. harteri* has not been collected. The region of the Brazos River along which Mr. Harter has taken *N. harteri* is 830 to 840 feet in altitude, while the other *Natrix* are at altitudes of 900 to nearly 1100 feet.

* Accurate count of body spots in one specimen not possible as it is in poor condition.

** For these localities, see Pickwick Quadrangle, Texas, U. S. Geological Survey.

Discussion: The writer was for more than a year reluctant to acknowledge the validity of this species. The first specimen was considered a freak offshoot of *N. e. transversa*. When it finally became apparent that snakes like the original distinct specimen actually formed a considerable population, nomenclatorial recognition of the entity seemed advisable. The possibility that this might be a race of *N. erythrogaster* was carefully considered and finally discarded, as Mr. Harter has clearly shown by his collections that *N. e. transversa* occurs in the same region, though in a different ecological niche, and that the snake which is here named *N. harteri* is a constant population showing no tendency toward intergradation in morphological characters with *N. e. transversa*.

The affinities of *N. harteri* are not as yet quite clear. The almost unmarked belly presumably relates it most closely to *N. erythrogaster* which is here

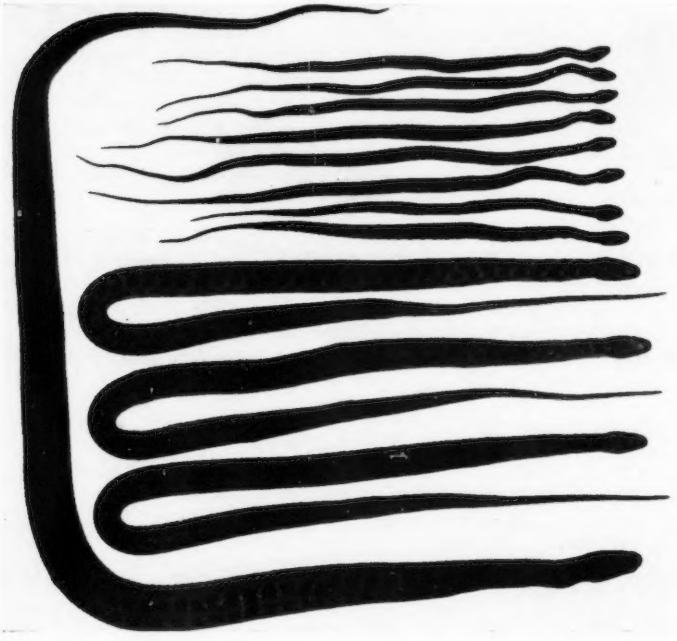


Fig. 5. A group of watersnakes, *Natrix*, from the vicinity of Palo Pinto, Texas. Included are ten paratypes of *N. harteri* n. sp. ranging in size from 295 mm. to 900 mm. and a young specimen of *N. r. rhombifera* and *N. erythrogaster transversa*. The latter are fifth and sixth from the bottom respectively. The uniform pattern of *N. harteri* and its distinctness from that of the other watersnakes of the region, as discussed in the text, is at once apparent.

reaching the western limit of its range. The dorsal pattern is totally unlike that of *N. erythrogaster* for it consists not of bands or of single dorsal blotches alternating with lateral ones, but of mostly alternating pairs of dorsal spots, alternating with lateral ones in much the fashion of *N. kirtlandii* and of some gartersnakes, *Thamnophis*, in which the stripes are suppressed and the checker pattern dominant (see Fig. 5). This pattern is strikingly similar to that of some *Thamnophis angustirostris* of the Mexican highland and portions of Arizona and New Mexico. The divided anal plate removes, however, the possibility of this snake being a *Thamnophis* although the narrow and elongate head is, in form, also more like that of a *Thamnophis* than a *Natrix*. The relationships of this species will probably be best worked out when more is known of its geographic range, and the direction of pattern variation, should such be found.

As yet the peculiar local endemism of this species admits of no ready explanation. The restriction of the species to the Brazos, once it had arisen, is perhaps understandable in the light of the large areas subject to extreme drought to both the north and the south, but it might also be expected that the periodic floods to which the Brazos is subject, along with other rivers of that region, would have carried *N. harteri* downstream to habitats not unlike that in which it thrives about Palo Pinto. Collections from Texas are as yet too sparse to admit of any satisfactory solution of the problem here raised. The relationships of *N. harteri* will be better understood when series of *Natrix* from the lower Brazos are available.

Acknowledgments: I am grateful to Dr. A. H. Wright for his interest and support which made it possible to secure the series of specimens of *N. harteri*, and much indebted to Miss Catherine D. Hemphill, who traveled far out of her way to secure habitat photographs and data, to Mr. Arthur L. Smith, for his expert assistance in preparing photographs, and to Mr. Philip Harter for his most enthusiastic and genuine interest in herpetology which brought this surprising novelty to light.

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Some Data on the Home Ranges and General Life History of the Short-tailed Shrew, Red-backed Vole, and Woodland Jumping Mouse in Northern Michigan

W. Frank Blair

Introduction

Some information about the home ranges and other phases of the life history of the short-tailed shrew *(Blarina brevicauda talpoides)*, red-backed vole *(Clethrionomys gapperi gapperi)*, and woodland jumping mouse *(Napaeozapus insignis frutectanus)* was obtained during a study of the home ranges of the woodland deer-mouse. These data are not sufficient for statistical treatment, but they do give some indication of the size of the home ranges of these forms.

The study was conducted on the Cusino State Game Area in Alger County, Michigan, from August 25 to September 22, 1940. I am greatly indebted to Adolph Stebler and Ford Kellum of the State Department of Conservation for many courtesies rendered during my stay in the area. J. S. Rogers, Jr., assisted in the field work. The field expenses were in part defrayed by the Laboratory of Vertebrate Genetics, University of Michigan.

Methods

Small live traps were set in a grid pattern in the midst of an extensive virgin hardwood forest. The intervals between the traps was 45 feet. The area actually covered by these traps comprised 18.18 acres. Near the close of the field work a line of traps, with the traps also 45 feet apart, was set 90 feet distant from the plot and entirely around it. These traps were set for 5 nights, and were used to determine which residents of the plot had home ranges extending beyond the regular trapping area.

The 18.18 acre plot itself was trapped for 28 days, between August 25 and September 22, 1940, but only one-half of the 432 traps were set at any one time. Alternating series of three lines each were set during alternate weeks. Thus, during the first and third weeks lines numbers 1, 2, 3, 7, 8, 9, 13, 14, and 15 were set. These were left unset during the second and fourth weeks, and lines numbers 4, 5, 6, 10, 11, 12, 16, 17, and 18 were set during those times. This method of trapping enabled us to catch each individual in more parts of its home range than would have been possible if all of the traps had been set simultaneously, for most small mammals tend to get into the traps nearest their homesites. If an animaal was caught in the same trap on two consecutive nights that trap was left unset on the third, thus allowing that individual to be caught in some other part of its home range.

The traps were left set continuously during the 7 days of each trapping period. They were visited in the morning and evening, and all captive mammals were removed, marked, recorded, and released at the point of capture. Most

of the shrews, red-backed voles, and jumping mice were in the traps in the morning, but on cloudy or rainy days red-backed voles and short-tailed shrews occasionally were taken. The traps were baited with sunflower seed except during the last week when rolled oats and peanut butter were added to the seed. The mixture seemed no more attractive to the small mammals than did the sunflower seed alone. A standard method of calculating the size of the home range (Blair, 1940a) has been used.

Blarina brevicauda talpoides

Twenty-eight short-tailed shrews were trapped on the plot. Of these, 16 were females and 12 were males, which indicated a fairly even sex ratio. Three of the females were young adults, but all of the other shrews were fully mature. Ten shrews were dead in the traps on the first night that they were caught. The others were trapped from one to 6 times each. The trapping records of these last give some indication of the minimum size of the home range of this species in a hardwood forest. Probably none of the shrews was caught a sufficient number of times, however, to show its entire home range.

One female that was caught 6 times had a calculated range of 1.46 acres, and two that were caught 5 times each had known ranges of 1.29 and 1.00 acres, respectively. Two others that also were taken 5 times each had known ranges of 0.59 to 0.56 acres, respectively. The range of the first of these two extended to the line 90 feet beyond the regular plot and therefore possibly beyond it. Three females that were trapped from two to three times each had known ranges varying from 0.09 to 0.51 acres. Two females were caught once and released, but never were retaken.

A male that was trapped 5 times had a calculated home range of 1.39 acres. One that was caught 4 times had a known range of 1.08 acres, but its range extended to the line 90 feet beyond the regular plot and therefore possibly beyond it. Five males that were captured from two to three times each had known ranges varying from 0.05 to 0.51 acres. One male was caught once and released, but never was recaptured. The data on the size of male and female ranges agree with previous observations (Hamilton, 1931:97) and (Blair, 1940b:286).

The calculated ranges of both males and females broadly overlapped the ranges of others of the same and opposite sex. Only one shrew showed any sign of sexual activity. A female that was trapped between September 16 and 21 had recently suckled young.

Clethrionomys gapperi gapperi

Nine red-backed voles were trapped on the plot. Of these, 5 were males and 4 were females. Three of the males were adults, one was a young adult, and one was immature. Two of the females were adults, one was a young adult, and one was immature. One of the adult females was caught 22 times and had a known home range of 0.57 acres. However, the range of this individual extended out to the line 90 feet from the regular plot, so part of the range possibly lay outside of the area trapped. The other adult and the young adult female were dead in the traps on, respectively, the first and second nights trapped. The immature female was caught only once.

One adult male was trapped 20 times, and had a calculated home range of 3.56 acres. Another was trapped 9 times, and had a known range of 0.49 acres. The other adult male was accidentally killed the third time it was caught, but after only three captures its known range comprised 1.61 acres. The young adult male was trapped 5 times, and had a known range of 0.62 acres. However, the range of this animal extended out at least to the line 90 feet away from the regular plot. The immature male was caught 9 times and had a known range comprising 0.59 acres, but its range also extended out to the line 90 feet away.

One adult male and female, the young adult female, and the immature male inhabited one part of the plot, where all of their home ranges broadly overlapped. The female of this group gave birth to a litter of young on the night of August 26, and again showed evidence of being pregnant when examined on September 16. The young adult female showed no sign of sexual activity. Sexual activity of the adult male was indicated by the enlarged testes, but the immature male was sexually inactive. Of the other red backed voles on the plot, the one adult female had recently suckled young, but the immature female showed no sign of breeding. The two adult and one young adult males were sexually active, as indicated by their enlarged testes. The active condition of the young adult male indicates that red-backed voles born during the summer may breed in late summer or early fall.

Napaeozapus insignis frutectanus

Fifty-two woodland jumping mice were trapped on the plot. Of these, 27 were females and 25 were males, which indicates that the sex ratio was about even. Thirty-two of the jumping mice were taken 5 or more times each. The calculated ranges for these animals are shown in Table 1. In order to determine the number of times that a jumping mouse had to be captured before the size of its entire range was known, the size of the known range of each mouse that was caught 10 or more times was plotted after each successive capture. This method previously has been used by Haugen (unpublished manuscript). Among 7 females in this group, the size of the calculated range of one individual failed to increase after the seventh capture, and with one animal there was no increase after the eighth catch. The ranges of two individuals failed to increase after their ninth captures. One female's range ceased to increase with the fourteenth capture, and one ceased with the eighteenth. The range of the one remaining female in the group showed a slight increase with her fifteenth and last capture. These calculations indicate that the number of captures necessary to learn the size of the entire home range varies greatly in different individuals. However, it is evident that at least 7, and sometimes as many as 18 captures are necessary. Of the three males that were taken 10 or more times, the range of one failed to increase after 9 catches, one showed no increase after 12 captures, and the other failed to increase after it had been taken 14 times.

In view of the above calculations, it seems evident that those home ranges in Table 1 based on less than 7 captures each must be regarded as only fractions of the actual ranges. In addition, some of those based on 7 or more cap-

TABLE 1.—Size of calculated home ranges of individual male and female *Napaeozapus* in hardwood forest, Alger County, Michigan, August-September, 1940.

Animal	No. times caught	Days between first and last catch	Calculated size of home range in acres	Animal	No. times caught	Days between first and last catch	Calculated size of home range in acres
♀ 70	22	25	*3.86	♂ 87	19	24	5.32
♀ 66	19	24	1.99	♂ 39	16	27	*4.67
♀ 81	15	24	3.10	♂ 122	15	20	*2.97
♀ 101	14	23	3.42	♂ 47	9	13	4.32
♀ 113	10	22	*1.22	♂ 127	9	19	*8.96
♀ 135	10	19	1.31	♂ 96	8	20	3.31
♀ 152	10	16	1.60	♂ 148	8	18	1.93
♀ 68	9	24	1.60	♂ 131	7	9	1.08
♀ 123	8	19	6.55	♂ 142	7	18	1.29
♀ 139	8	13	2.95	♂ 153	7	9	2.17
♀ 125	7	18	*2.72	♂ 178	7	12	1.13
♀ 132	7	10	1.05	♂ 147	5	18	3.53
♀ 109	6	19	3.17	♂ 160	5	15	1.53
♀ 156	6	16	2.09	♂ 170	5	11	0.56
♀ 141	5	18	1.02				
♀ 143	5	6	0.58				
♀ 175	5	11	2.85				
♀ 179	5	11	1.46				

* Range extended out at least to line 90 feet beyond regular plot, so ranges possibly are not complete.

tures possibly are fractional also. The home range data do indicate, however, that the range of the woodland jumping mouse is relatively large and that it varies greatly in different individuals. The ranges of the females appear to vary from about 1.0 to 6.5 acres, while those of the males comprise from about 1.0 to 9.0 acres. The data suggest that the males tend to range somewhat more widely than the females. The largest male range considerably exceeded the largest range of a female, and the three next largest male ranges were larger than all but the largest female range. The home ranges of both males and females broadly overlapped.

The breeding season was nearing its close when trapping was begun August 25. Of 9 females examined during the first week, 4 adults apparently were pregnant, two other adults recently had suckled young, and two adult and one young adult females were sexually inactive. No other breeding females were seen during the subsequent weeks of trapping. One of 4 males examined during the first week was sexually active, as indicated by the enlarged testes. However, the testes of this individual were small during the three subsequent weeks of trapping, and no other male with enlarged testes was examined. All of these data indicate that the breeding season ended about the last of August.

Bot-fly larvae were found beneath the skin of 5 of the 25 males, and 7 of the 27 females. The larvae usually were in the inguinal region, but one was in the dorso-lumbar region.

Many of the jumping mice had become very fat before the trapping ended on September 22, 1940, evidently in preparation for hibernation. None of the

4 males and 9 females examined in the first week was fat, but in the second week one of 13 males and two of 20 females were fat. In the third week only two of 17 males were fat, but 10 of 21 females were fat, which suggests that the females start getting fat slightly earlier than do the males. In the fourth week 8 of 19 males and 9 of 21 females were fat. The most obese individuals were much clumsier than the lean ones, and presumably much more easily captured by predators.

One jumping mouse presumably was killed by a weasel (*Mustela* sp.) which forced open the trap door and killed the mouse after which it devoured the brains. On one occasion an adult male woodland jumping mouse and a young adult male deer-mouse were taken in the same single-catch trap. With this type of trap it was necessary that both enter the trap at the same time. There was no evidence of any fighting between the two, and when removed from the trap they appeared to be living amicably together.

Summary

Twenty-eight short-tailed shrews *(Blarina brevicauda talpoides)*, 9 red-backed voles *(Clethrionomys gapperi gapperi)*, and 52 woodland jumping mice *(Napaeozapus insignis frutectanus)* were among the small mammals trapped from August 25 to September 22, 1940, on an 18.18 acre plot in a virgin hardwood forest in Alger County, Michigan. The few data available indicate that in such a situation the home range of the short-tailed shrew usually exceeds one acre. The home range of an adult male red-backed vole sometimes may comprise as much as 3.56 acres. The size of the range of the woodland jumping mouse is variable, but an adult male sometimes may range over as much as 8.96 acres, while an adult female may range over as much as 6.55 acres. In all three species, the ranges of both males and females overlapped the ranges of other individuals of both sexes.

Only one shrew showed any sign of recent sexual activity, but the red-backed voles were actively breeding. Breeding activity in the woodland jumping mouse ended near the last of August. Several of the jumping mice were infested with bot-fly larvae, but no larvae were found in either of the other two species. In early and middle September, the jumping mice were becoming fat in preparation for hibernation.

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Notes on Some Mammals of Lee County, Florida

W. J. Hamilton, Jr.

The mammal life of Florida is but imperfectly known. The late Arthur H. Howell has made numerous extensive collecting trips to various parts of the state, but few of the accumulated data have been published. Sherman (Proc. of the Florida Acad. Sciences for 1936, vol. 1, pp. 102-128) has listed the recent land mammals of Florida and their known distribution up to 1936. His paper contains a very complete bibliography on the distribution of Florida mammals.

I spent the period of March 28-April 4, 1939, and March 23-April 5, 1940, in the vicinity of Fort Myers, Lee County, Florida. While collecting was mainly confined to amphibia and reptiles, some mammals were secured. In addition to these short periods, my wife and children were in this region for the entire winter and spring of 1939 and 1940. They collected a number of interesting specimens and kept detailed notes on the mammals. Mr. Dwight Dyess, a lifelong resident of Lee County, has provided me with interesting accounts of the larger forms. I spent several profitable days in the field with him.

Specific accounts of the forms listed below are notable only for their paucity. While the present list makes no pretense at completeness, it does include data of an unpublished nature which add in a small measure to our knowledge of these species.

Didelphis virginiana pigra. Florida opossum. Generally distributed throughout the county. Many are killed on the Tamiami Trail, but one must visit the highways at daybreak to see the casualties for the buzzards make short work of them. Opossums are very bold, entering chicken houses and causing a heavy loss. Dyess killed six in one week at Halfway Pond, but all were thrown away, as the pelts are seldom worth more than 25 cents.

Scalopus aquaticus bassi. South Florida Mole. This recently described little mole, previously known only from the type locality, Englewood, Sarasota County, is common about Fort Myers. Its characteristic little mounds are particularly abundant in lawns, golf links and waste areas. The late Arthur H. Howell, who described this mole, wrote me that additional specimens have been taken at Jupiter, Lake Worth and Miami. Thus the known range of this smallest *Scalopus* extends across the southern part of the peninsula north of the Everglades.

The single specimen which I have examined was a male collected on February 11, 1940. It had small testes. The measurements are, total length, 112 mm.; tail, 12 mm.; hind foot, 17 mm. The specimen weighed 37 grams. The stomach contained several lepidopterous larvae.

Cryptotis floridanus. Florida Short-tailed Shrew. On March 25, 1940, I collected a single individual in the runway of a cotton rat. It was a male with enlarged testes and prominent side glands. The following day an adult female was secured. It showed no indication of breeding. The stomachs of both speciments contained the fragmentary remains of insects.

Tadarida cynocephala. LeConte Free-tailed Bat. As the oldesct fronds of the Washingtonia palms die, they bend near their base, to form a heavy canopy and an ideal retreat for many animals. In early April of 1940 I was vigorously shaking such a mass to frighten any lizards which might be in hiding when a bat flew from the retreat. It was soon followed by several others. While I was unable to collect these, their strong swift swallow-like fllight and color indicated them to be free-tailed bats. These were the only bats I was able to identify, although several others were seen in the twilight.

Euarctos floridanus. Florida Black Bar. The black bear is still tolerably common in the wilder portions of the country. It frequents the hammocks and higher ground generally although it has no hesitancy in entering the cypress

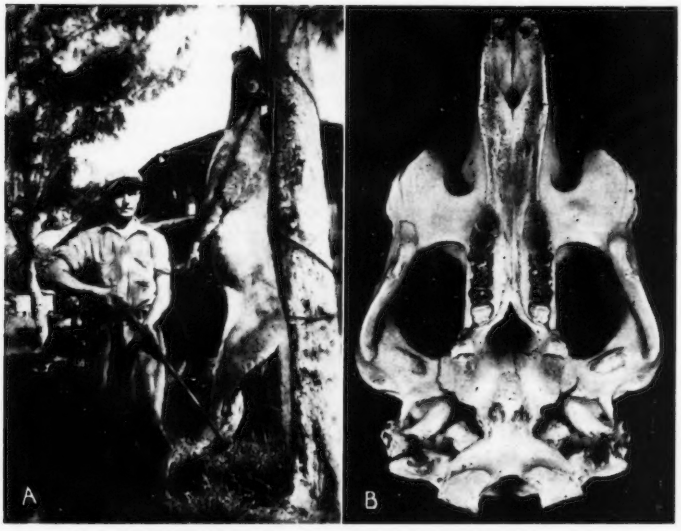

Fig. 1. A. Panther killed by Mitt McSwain on October 10, 1939 one mile from Bonita Springs, Lee County, Florida. B. Skull of adult female *Trichechus latirostris* collected February 11, 1940 in the Caloosahatchee River, 10 miles above Fort Myers. It is presumed that the animal was killed by the low temperatures prevailing two weeks earlier. The wear of the molar teeth and their eventual loss may be seen. It is said that the incisors are present in the fetal stage. What are presumably incisor sockets are present, but there was no evidence of vestigial teeth even beneath the gums in this individual.

swamps. A few are killed in Lee and surrounding counties each year. Dyess does not believe the bears become dormant here although it is known that in northern Florida the females are lethargic for several months during the coldest part of the winter. Bears prepare a bed on the ground in dense thickets, pulling together grass and moss which they tread down.

Their food is chiefly of vegetable origin. Acorns, cabbage palmetto berries and buds are important food. A large bear will climb to the top of a cabbage palmetto, put his arms around the top and sway back and forth until the big bud loosens, then fall to the ground on his back, the tender cabbage securely grasped in his paws. The cabbage is said to be an excellent laxative and tonic. The Florida black bear is particularly destructive to pigs and nearly grown hogs. According to Dyess, an individual will follow a drove, killing and eating the pigs until the drove is entirely destroyed.

Procyon lotor elucus. Florida Raccoon. The raccoon is common throughout the county, particularly so about the tidewater, where the dense mangrove swamps provide an abundance of food in the form of innumerable crabs and frogs. I saw numerous tracks in the swamps near Fort Myers Beach, and on the sandy roads leading far into the hammocks. On April 1, 1940, the soft-shelled turtles *(Amyda ferox)* were repairing to these roads in great numbers to lay their eggs. Several were seen in the act of deposition. More than fifty nests had been rifled by raccoons and foxes, as the abundant testimony in the form of tracks indicated. The raccoon is trapped in some numbers, but its pale yellow pelt is not of great value, average skins selling for a dollar, while the best pelts fetch $2.50.

Spilogale ambarvalis. Florida Spotted Skunk. The little spotted skunk is quite abundant. A pair lived under the garage of a neighboring residence, and each evening at dusk they would come out to play, rolling about like kittens or searching for garbage. I trapped a female on April 4, 1940, which weighed 712 grams. It had no embryos. The stomach contents contained the remains of a skink *(Eumeces inexpectatus)* and a mass of dirt and sticks, with a few fragmentary insect remains. The effluvium from the anal glands are nearly as powerful as that of the big northern skunks. These little "civets" are seldom trapped for their fur, the pelts averaging about 25 cents.

Several grove owners and farmers told me that a large striped skunk *(Mephitis elongata?)* was occasionally killed near Fort Myers.

Urocyon cinereo-argenteus floridanus. Florida Gray Fox. Abundant in Lee County. The gray fox is an important game species, and is hunted during the winter and early spring. Dogs are employed, and the hunters either use horses or crowd into a truck especially adapted for use in the swamps and rough country. The animals often give the dogs a long chase, and do not always take to a tree. When run down they are either shot or taken alive. The pelts are of little value.

Felis concolor coryi. Florida panther. The panther still occurs in the wilder

parts of Lee, Collier and Hendry counties. The panthers are said to feed on deer, pigs, young calves, rabbits, turkeys, etc. In July, 1940, Dyess was riding in the hammocks about 17 miles east of Fort Myers when he came upon a half eaten pig. He had followed the lion sign until he came on the still warm body of a grown sow. This had been pulled back into the palmettos with several branches covering it. Dyess has found where gravid does have been killed by a lion and the foetus removed and eaten. A mare with colt will likewise be killed and only the foetus eaten.

Panthers have been especially destructive to cattle since the deer eradication campaign was instigated in lower Florida in an effort to control the fever tick. As a consequence, more are being hunted than formerly. According to Ransom Page, two panthers were killed near Naples during late November, 1939. A large specimen was shot by Mitt McSwain on October 10, 1939, just a mile from Bonita Springs. This animal weighed 145 pounds after considerable loss of blood. A larger individual was shot near Estero on November 20, 1939. This animal weighed just slightly less than 200 pounds.*

The ever increasing destruction of deer in these lower counties may eventually spell the doom of the panther in its last eastern stronghold.

Lynx rufus floridanus. Florida Bobcat. The bobcat is common in Lee County. Hunters and cowmen occasionally kill them. The pelt has little value and is not sold. I saw several pelts which had been taken by fox hunters.

A pair of black bobcats were trapped by the Marcum brothers between Clewiston and Belle Glade, Palm Beach County, and the skins are now in the possession of A. A. Harrington of LaBelle. The fur is dark brown shading to black on the back and speckled with white hairs. The spots are visible when the skin is held at an angle. The cats were trapped in February, 1940.

Sciurus carolinensis extimus. Everglade Gray Squirrel. A gray squirrel was seen on April 1, 1939, just outside the limits of Fort Myers.

Sciurus niger avicennia. Mangrove Fox Squirrel. My wife saw a fine example of this species not far from Fort Myers, in a thicket bordering a small cypress swamp. I saw a reasonably tame individual near Tice, but was unable to collect it.

Sigmodon hispidus littoralis. Florida Cotton Rat. The cotton rat is the most abundant rodent in Lee County. Its numerous runways and trails thread all suitable cover and where a canopy of grass and matted growth provide suitable cover, it becomes extraordinarily abundant. My son counted eleven rats that ran from a small plot of dense grass less than a quarter acre in extent when this was fired. Three males which I trapped in late March and early April, 1940, had much enlarged and descended testes. Two adult females taken at the same time showed no signs of sexual activity.

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* On April 3, 1941 a cowhand shot a large female near Immokalee. This was exhibited with its two live kittens in Fort Myers on the same day.

Rattus rattus alexandrinus. Roof Rat. The remains of several of these rats were seen, and a large male in a diseased condition was killed by my son in the garage.

Sylvilagus palustris paludicola. Florida Marsh Rabbit. While cleaning a ditch near the southern limits of Fort Myers on March 23, workmen captured two young marsh rabbits which scurried from their shallow nest. On the same day, a nest of five young with unopened eyes was found beneath a cabbage palm. In this immediate area, several large diamond-back rattlesnakes were killed on various days. It is suspected that swamp rabbits provide a substantial part of the food of these big snakes.

On March 30, 1940, I saw a third grown marsh rabbit crouched beneath a lumber pile. For five successive days this rabbit was observed in the same form. A half grown individual was observed one evening at dusk. From the size of these two individuals, I should judge that breeding occurs as early as January. Rabbits are little hunted in these parts.

Odocoileus virginianus osceola. Florida Deer. In spite of the extirpatory campaign against deer in the lower counties, and limited year round poaching in Lee County, deer are still fairly common. Numerous tracks were seen in the pine woods and cabbage palm thickets bordering the smaller cypress swamps. The fawns are born from late January to early March. Dyess saw a buck, two does and two fawns on March 29, 1940. The buck had just commenced to grow new antlers, the velvet stubs being scarcely three inches long. Unusually large bucks weight about 150 pounds when hog dressed.

In general, the deer are considerably smaller than those from the north. However, I saw some mounted heads of large bucks in a taxidermist's shop in Fort Myers, the antlers of which compare favorably in size with large specimens from New York.

Trichechus latirostris. Manatee. Seacow. The manatee is not uncommon in the Caloosahatchee River, ascending nearly fifteen miles above Fort Myers. Cahn (Jour. Mammalogy, 21(2):222-223) has recorded the mortality of these interesting beasts during the Florida freeze of January, 1940. He states that five were found dead in the vicinity of Charlotte Harbor, following a three day period in which the air temperature hovered afound 19° F. and the water temperature dropped from 68° F. to 46° F. The press carried stories of this mortality and in this manner my wife managed to track down, after considerable effort, a large manatee which had died in the Caloosahatchee about ten miles up river from Fort Myers. This animal, a huge female, was estimated to weight 1200 pounds and exceeded ten feet in total length. The skull was removed and is now in the collection of Cornell University.

The bones of the manatee are unusually dense and heavy. The skull of the female mentioned above weighed 11 pounds; in contrast to this the skull of a dolphin of comparable size weighed 3.52 pounds. *Trichechus* is remarkable among the Sirenia in having a progressive succession of the molariform teeth comparable to the condition found among elephants. This constant displace-

ment of the fore teeth and eventual eruption of new back molars apparently continues throughout life, as the accompanying figure illustrates. Thomas and Lydekker (Proc. Zool. Soc. London for 1897, pp. 595-600) have suggested the possibility of not less than 20 teeth in each series during the life span of *Trichechus*. In the specimen at hand, the first two in each side of the upper jaw and the first pair in the lower jaw dropped from their shallow sockets when the skull was cleaned. They are so worn that no indication of the tubercles persist, indeed the surface of the worn first few teeth are concave, contrasting markedly with the prominent tubercles and convex appearance of the little worn hind molars. It appears probable that this wear is occasioned by the nature of the food. Aquatic plants generously mixed with sand from the river bottom would cause abrasive loss of the crowns.

The manatee is said to calf in the late winter, repairing to the larger rivers for parturition. The young are of good size by late summer.

There may be a short emigration in this species in the Fort Myers region. Several boatmen about Punta Rassa told me that sea cows were seen in the mouth of the Caloosahatchee River in January but not at other seasons. Possibly they ascend the river for breeding at this time.*

Tursiops truncatus. Bottlenose Dolphin. These cetaceans are common near Punta Rassa, in the mouth of the Caloosahatchee River. A school of seven were seen here on April 4, 1940. Two large individuals were accompanied by their calves, the youngsters swimming just behind the fore flipper and so close that they appeared to be attached to the parent. Both parent and young breach together in perfect unison. In the bay at Fort Myers Beach, several dolphins were observed leaping clear of the water to a height of ten feet or more, falling gracefully back head first or landing on their sides with a resounding splash. As the dolphin breaks water, it emits a pronounced "whish."

Globicephala brachyptera. Short-finned Blackfish. On April 5 and 6, 1939, several small schools of blackfish were seen in the bay at Fort Myers Beach. One lot of seven individuals swam directly beneath the motor bridge and it was possible to observe them clearly. I estimated their length at from 14 to 18 feet. Blackfish occasionally break into the fish nets but the fishermen believe this to be accidental, with no design on the captured fish. This species occurs in the Caloosahatchee River several miles above Fort Myers.

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* Captain Don Waters witnessed the "natural" death of a manatee in Orange River. The skull was saved and later presented to me. The animal measured nine and a half feet and was estimated to weigh 1000 pounds.

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Two New Middle Pliocene Carnivores from Oklahoma With Notes on the Optima Fauna

Donald E. Savage

This paper is concerned with a description of two new carnivores near Optima, Oklahoma, and the vertebrate fauna of the Middle Pliocene deposits at that locality. The description of this fauna has been used as a master's thesis at the University of Oklahoma. Most of the specimens discussed in this report were collected by W.P.A. labor under the sponsorship of the University of Oklahoma in 1937 and 1938. Previous to that time scientific parties from the University of Oklahoma, University of California and the Frick Laboratories of the American Museum of Natural History obtained material from the Optima locality.

The writer wishes to express his appreciation to Dr. J. Willis Stovall of the University of Oklahoma for aid in the diagnosis of specimens and criticism of the manuscript. Through the generosity of the late Mr. C. Stuart Johnston of the West Texas State College, Canyon, Texas, access was gained to the Middle Pliocene collections from the Texas Panhandle, housed in the Panhandle Plains Historical Society Museum. The writer is also indebted to Mr. Ralph B. Shead, artist for the Museum of Geology and Paleontology at the University of Oklahoma, for constructive criticisms of the drawings accompanying this description.

Geology of the Beds

The Optima beds are Middle Pliocene in age and occur as streaam channel deposits in a widespread blanket of Late Tertiary sediments. These Tertiary sediments are composed of gravel, conglomerate, sand, sandstone, silt, clay, with minor amounts of volcanic ash, sub-bentonite and diatomaceous marl. Caliche ($CaCO_3$) is intercalated with these deposits. This heterogeneous assortment of deposits covers all of Texas County except relatively small exposures of red Permian clastics along the Paloduro Creek in the southeastern part of the county and an inlier of Mesozoic rocks at Red Point, ten miles west of the Optima locality, on the Beaver River. The relationships of this Late Tertiary blanket of sediments are so obscure that a definite age may be assigned only to those beds bearing fossils. The fossiliferous deposits at Optima are exposed in the escarpment eroded by several small intermittent streams draining southward into the Beaver River. Due probably to loose cementation in the caliche cap rock, the escarpments are not prominent, but assume more the form of steep, talus-covered slopes and rolling hills.

The five quarries from which the University of Oklahoma parties collected are all included in an area of less than 160 acres. Throughout this small area

the stratification remains fairly uniform. The following section shows the relationship of the fossiliferous to non-fossiliferous strata.

	Feet
Soil and caliche	3 - 7
Buff to grey clay and silt (fossils)	7 - 8
White quartz sand, grades into grits and gravel in places (fossils)	4 - 7
Brownish-red sand, grit and gravel	2 - ?

Most of the fossils have been found in the white sand member.

Geologists have long realized that the determination of exact relationships between Cenozoic rocks in any part of the High Plains is a complex problem. This problem is characteristically difficult in Okahoma. No individual bed ever constitutes a mappable unit. The Tertiary rocks in Oklahoma lie uncomformably upon formations of Permian, Triassic, Jurassic and Cretaceous age. Many names have been used in the literature in an attempt to classify chronologically the various exposures of Tertiary in the Oklahoma Panhandle and adjoining regions. Most of these terms, however, have been discarded. LATE TERTIARY is the term applied when absence of fossil evidence anl lack of lithologic peculiarities warrant a no more specific designation. The term OGALLALA FORMATION is used when similarities in fauna, flora and lithology between the Oklahoma deposits and the type Ogallala formation near Ogallala, Nebraska, can be ascertained. Although Darton (1903) described and named the Ogallala, he designated no type section for this formation. In an oral communication with Stirton (1936b), Elias proposed a type section for this formation in the exposures in the canyon two miles east and one-half mile north of the town of Ogallala on the Feldt Ranch. Hesse (1935) had named the vertebrate assemblage at this type locality the "Feldt Ranch Fauna." The presence of *Hypolagus, Dipoides, ?Osteoborus, Felis, Teleoceras, Neohipparion, Calippus* and *Prosthennops* at Feldt Ranch demonstrates that the type section of the Ogallala is Middle Pliocene in age. Notwithstanding the fact that the type Ogallala is Middle Pliocene, this formation term is today applied to the whole thickness of predominantly arenaceous Late Tertiary beds on the High Plains. Consequently, through its generalized usage, the name Ogallala has included beds of Upper Miocene to possibly Pleistocene age. In Oklahoma the Ogallala formation is limited to the Pliocene, for no evidence of Miocene age has yet been found in any of the Tertiary sediments of this state. Out of the confusion which has arisen over the stratigraphy of the High Plains one fact has made itself apparent: Lithology is an extreme unreliable criterion for correlation between members of continental Pliocene formations.

Description of the Optima Material

REPTILIA

CROCODILIDAE gen. et sp. indet.

The presence of an alligator in the Optima fauna is denoted by a single tooth and one dermal plate.

MAMMALIA

DIDELPHIIDAE gen. et sp. indet.

Plate 2, Fig. 7

An upper canine indicates the possible occurrence of this family in the Optima fauna. The Pliocene tooth was compared to similar teeth in six recent skulls of *Didelphys virginianus* in the Museum of Paleontology at the University of Oklahoma. It was found to be slightly larger than the canines of the recent individuals, being also more compressed than *D. virginianus*. This canine tooth is not to be confused with a deciduous cat or mustelid canine since it is but a simple, hollow, curved cone, compressed along the posterior edge.

CANIDAE

Osteoborus cyonoides (Martin)

Plate 1, Fig. 10

This hyaenoid dog from the Optima locality is represented by many lower jaws, portions of skulls, limb bones, vertebrae, and scores of individual canine, premolar, molar and incisor teeth. The writer was fortunate in being able to compare the aggregate of *Osteoborus* material of the University of Oklahoma with an excellent series of *O. cyonoides* specimens of the Hemphill fauna in the West Texas State College collection.

Vulpes stenognathus n. sp.

Plate 1, Figs. 1-5

Canis, Leidy

Leptocyon, Matthew, Bull. Amer. Mus. Nat. Hist., Vol. 38, (1918), pp. 183-229.

?*Vulpes*, Stirton, Amer. Jour. Sci. Vol. 32, (1936), p. 170.

Cotypes: O.M.P. No. *40-4-S24*, a right ramus with dentition, P_2-M_2 inclusive; ascending ramus and symphyseal region absent. O.M.P. No. *40-4-S16*, portion of a right ramus including P_1-P_4.

Paratypes: M_1—two specimens; M^1—four specimens; M^2—two specimens.

Etymology: Greek, στενός—"narrow"; γνάθος—"jaw."

This name is given in reference to the relatively compressed ramus of this animal.

Diagnosis: Jaws slender, compressed, deeper than recent species of *Vulpes* and *Urocyon;* premolar region relatively long, premolars well spaced and compressed, with reduced accessory cusps; larger than most living species of *Vulpes* and *Urocyon;* M^1 and M^2 show same cusp arrangement as *V. fulvus*.

Description: The specific type *"Leptocyon" vafer* Matthew (1918) was described from the Snake Creek fauna of Nebraska, but no figures or measurements were given. *V. stenognathus* agrees with all the characters given for *"L." vafer* except that the accessory cusps on the premolars of *V. stenognathus* are subordinate or vestigial. The rami of *V. stenognathus* were compared to *Vulpes fulvus* (Recent) in the University of Oklahoma collection and to *V.*

macrotis and *Urocyon cinereoargentatus* (Recent) in the West Texas State College collection. It was noted that the accessory cusps on the premolars of *V. fulvus* and *U. cinereoargentatus* have been so reduced that they are merely swellings on the anterior and posterior sides of the median cusp. In this character *V. stenognathus* is apparently more closely related to the two living genera than to *"Leptocyon" vafer*. A fox in the Hemphill fauna, *?Vulpes* sp., Stirton, is larger and the jaw is not so deep nor so compressed as *V. stenognathus*. None of the genera studied have the same degree of lateral compression in the horizontal ramus as that seen in *V. stenognathus*. There is at least a difference in species between the Optima fox and the Hemphill fox. The following table shows the dimensions of the cotypes of *V. stenognathus* with comparative measurements of *V. fulvus*.

Measurements in Millimeters

	V. stenognathus 40-4-S10	*V. stenognathus* 40-4-S24	*V. fulvus*
Diameters of M^2, antero-posterior × transverse	12.8 × 5.8	12.1 × 5.5	12.7 × 5.7
Length, P_2-P_4 inclusive	28.5	26.5	19.8
Length P_1-P_4 inclusive	35		24.5
Length, M_1-M_2 inclusive		21	19.5
Diameters of M_2, antero-posterior × transverse		7.5 × 5.8	6.9 × 5.3
Diameters of M_1		13.9 × 5.5	12.7 × 5.7
Diameters of P_4	9.4 × 3.5	9.4 × 3.6	7.9 × 4
Diameters of P_3	8.6 × 2.8	8.2 × 2.6	5.9 × 2.8
Diameters of P_2	7.7 × 2.5	7.1 × 2.4	5.5 × 2.6
Diameters of P_1	3.3 × 1.1		2.9 × 2.1
Depth × thickness of jaw below P_2	12.8 × 5.8	12.1 × 5.2	
Depth × thickness of jaw below P_4	13.7 × 6	14 × 5.5	
Depth × thickness of jaw below M_2		? × 5.1	

Two specimens of M^1 and M^2, listed as paratype material, were compared to similar teeth in *V. fulvus*, *V. macrotis* and *U. cinereoargentatus*. It may be seen from the following table that *V. stenognathus* has larger upper molars than the living genera of foxes.

Measurements in Millimeters

Diameters of M^1 antero-posterior × transverse:

stenognathus		*Vulpes*		*Urocyon*
40-25-S1	40-25-S2	*fulvus*	*macrotis*	*cinereoargentatus*
9.2 × 11.3	8.4 × 11.3	8.5 × 11.1	8.5 × 10.5	8 × 10.5

Diameters of M^2 antero-posterior × transverse:

stenognathus		*Vulpes*		*Urocyon*
40-25-S1	40-25-S2	*fulvus*	*macrotis*	*cinereoargentatus*
5.3 × 8.2	6.2 × 9.5	5.4 × 8.6	5.2 × 7.8	5.4 × 8

In M^1 of *V. stenognathus*, *V. fulvus* and *U. cinereoargentatus* the protocone and paracone are the most prominent cusps, the protoconule and the

metacone are well developed, but the hypocone is reduced and subordinate. The ectostyle is well developed, with parastyle slightly cuspate. In M^2 of these three species the protocone and paracone are the largest and most effective cusps; the protoconule is well developed, but the metacone is reduced as compared to the important metacone of M^1; the parastyle, mesostyle and metastyle form a continuous crest as in M^1 but this feature is more shelf-like in M^2.

URSIDAE

Agriotherium schneideri Sellards

Plate 2, Figs. 8-14

Agriotherium, Wagner, 1837.
Hyaenarctos, Falconer and Cautley, 1845.
Agriotherium schneideri, Sellards, Rept. Florida Geol. Surv., Vol. 8, (1916), pp. 77-119.

This ursid is represented by the left ramus of a young though full grown animal and by several upper and lower molars, premolars and incisors. The ramus is incomplete since the upper and anterior portions of the jaw have been scaled off, exposing the permanent P_4, M_1 and the canine. In life this individual had probably only begun to cut these teeth. Anterior to P_4 there are three alveoli, the median one bearing a tooth. The anterior and posterior alveoli, probably contained deciduous teeth. The actual depth of the jaw is nearly as great as the distance from the top of the protoconids of P_4 and M_1 to the base of the ramus. In this animal the premolars are reduced, but the molars are greatly developed. M_1 is blunt and powerful but the protoconid and paraconid make effective shearing blades. *A. schneideri* from Optima is very similar to *A. schneideri* from Bone Valley, Florida, in that P_4 is over half as long as M_1; the metaconid of M_1 is reduced and placed well behind the protoconid; the hypoconid is much larger than the entoconid and receives the heaviest wear of any part of the talonid. The Optima bear differs in a distinguishing feature from *A. schneideri* in that M_2 has the greatest width of any tooth in the lower jaw. In *A. schneideri* from Florida the heel or talonid of M_1 shows the greatest width of the lower dentition. As pointed out by Sellards (1916), the character of a greater width in M_2 is common to all the modern bears. The following table shows comparative measurements between *A. schneideri* from Florida and Optima respectively.

	Florida specimen	Optima-specimen O.M.P. No. *33-4-S1* 87
Length of molar series	90	
Diameters of M_1, antero-posterior × transverse	26 × 20	45.5 × 23.5
Diameters of M_2	26 × 20	32.5 × 25.1
Diameters of M_3	20 × 12	19.8 × 17.7*
Diameters of P_4	22 × 14	25.7 × 14.5

* Measurement taken from a non-associated tooth in the Optima collection.

A right M^2 in the University of Oklahoma collection is quite close to a M^2 identified by Matthew (1924) from the Snake Creek fauna as *?Hyaenarctos* sp. and figured by Frick (1926) under the subgenus *Lydekkerion*. The tooth is low-crowned and the external cusps make a sharp angle postero-inter-

nally. The paracone and hypocone are well developed, but the protocone and metacone are considerably reduced. The tooth bears the appearance of being laterally compressed through the protocone and paracone. The antero-internal border is greatly depressed.

A left M^1 was compared to figures of the same tooth in "*Hyaenarctos*" *schneideri* given by Frick (1926) and it was found that the Optima molar is much longer and narrower. The lingual cusps of *A. schneideri* from Optima (protocone and hypocone) are apparently much more prominent than on any figured species of *Agriotherium*. Likewise the lingual angles of the tooth are less rounded and are more prominent than any figured species; however, the diagnostic strength of this character is probably of minor importance. One of the characters of the subgenus *Lydekkerion* of Frick was the presence of a much higher paracone than metacone on M^1, especially in contrast to the relationship of these two cusps on M^1 of the genus *Hyaenarctos*. On the molar from Optima the paracone is much higher than the metacone, although the metacone is a much larger and stockier cusp. The M^1 of *A. schneideri* from Bone Valley apparently has the same size and height relationship of these two cusps as the Optima animal, as far as is determinable from Frick's figure. Frick apparently interpreted the size of the metacone as being indicative of the height of the cusp and accordingly placed *A. schneideri* under the genus and subgenus *Hyaenarctos*, since a higher metacone than paracone was a distinctive character of that subgenus.

FELIDAE

Machaerodus catocopis Cope

Plate 1, Fig. 8

A left ramus, several upper canine teeth, upper and lower cheek-teeth including carnassials, a metapodial and an astragulus have been referred to this genus and species.

Machaerodus (Heterofelis) coloradensis (Cook)

Plate 1, Figs. 9, 9a

A left M_1, O.M.P. No. *36-26-S2*, is referred to this species erected by Cook (1922). In contrast to *M. catocopis* this tooth shows a prominent and fully-developed metaconid, a character on which Cook based his genus *Heterofelis*. Matthew (1924) doubtfully left *Heterofelis* as a valid subgenus but referred *H. coloradensis* to *M. catocopis*, saying that the metaconids on Cook's specimens were all damaged and the evaluation of the prominence of these cusps was impossible. However, there is no question of the presence of a metaconid on the Optima specimen for it is perfectly preserved and agrees with Cook's description. The protoconid and paraconid of this tooth are well developed and are machaerodont-like in that they are inclined very little to the posterior. The general proportions and position of these two cusps are

closer to *Machaerodus* than *Ischyrosmilus* or *Smilodon*. If this tooth remains in the genus *Machaerodus*, a revision of the characters of this genus given by Burt (1931) is necessitated, for Burt made the absence of a metaconid on M_1 one of the diagnostic features of the genus. The following table shows comparative measurements between *(M. Heterofolis) coloradensis* from Yuma County, Colorado, *M. catocopis*, and *M. (Heterofelis) coloradensis* from Optima.

	Yuma County			Optima		
	No.	No.	No.	No.	*M.*	*M.(H.)col-*
	207	208	209	210	*catocopis*	*oradensis*
Length, M_1-P_3 inclusive	74	81	88	86*	76.2	
Antero-posterior diameter of M_1	30		36	33*	30.5	32.6
Transverse diameter of M_1	12			14	12.5	14.1
Antero-posterior diameter of P_4	21	23	30	28*	27	
Transverse diameter of P_4	9	10			11	
Antero-posterior diameter of P_3	19	20	24*	20*	18.8	
Transverse diameter of P_3	6	9			7.6	

* Indicates approximate measurements.

Felis proterolyncis n. sp.

Plate 1, Figs. 6, 7

Cotypes: O.M.P. No. *36-4-S2*, a right ramus with M_1-P_4 included. O.M.P. No. *36-4-S11*, a right ramus with P_4-P_3 included.

Etymology: Greek, *πρότερος*—"former"; *λύνξ*—"lynx."

Diagnosis: Size comparable to *Lynx rufus;* ramus stockier than *Lynx;* close spacing of the cheek-teeth causing a relatively shorter molar-premolar length than in *Felis* or *Lynx;* accessory cusps on P_3 and P_4 not so prominent as in *Lynx rufus, Felis leo,* or *Felis domestica;* greater separation of the paraconid from the protoconid of M_1 than in *F. leo, F. concolor, F. domestica,* or *Lynx rufus.*

Description: In specimen No. *36-4-S2* P_3 was evidently lost during life for the alveolus is partially sealed up by bony growth. The posterior portion of the symphysis of this jaw is present and shows the alveolus for a relatively large canine. The short jaw indicates that the animal was typically felid. The cotype, No. *36-4-S11,* contains P_3 which was absent on the other jaw. This ramus exhibits relatively unworn teeth while the other jaw shows a well-worn dentition. The size, mandibular construction and tooth structure of *F. proterolyncis* place this genus very close to *Lynx.* The following table of measurements compares *Felis proterolyncis* to three mandibles of *Lynx rufus.*

	Lynx rufus			*Felis proterolyncis*	
	36-0-5	*36-0-4*	*36-4-S8*	*36-4-S2*	*36-4-S11*
Length, M_1-P_3 inclusive	30.9	30.9	29.8	27.5	
Depth of jaw anterior to P_3	14.7	15.2	13.9	14.3	15.3
Depth of jaw below posterior cusp of P_4	16.8	16.8	15.2	16.4	
Thickness of jaw below P_3	7.5	7.4	6.5	7.8	7.8
Thickness of jaw below paraconid of M_1	7	7.6	6.5	7.7	
Antero-posterior diameter of M_1	13.2	12.9	12.5	12.5	
Transverse diameter of M_1	5.7	5.5	5.2	5.6	
Antero-posterior diameter of P_4	10.1	10.9	9.8	10.4	10.2
Transverse diameter of P_4	4.8	4.9	4.6	4.9	5.2
Antero-posterior diameter of P_3	8	8.1	7.9		8.2
Transverse diameter of P_3	4.3	4.4	4		4.4

EQUIDAE

Pliohippus interpolatus (Cope)

The Equidae from Optima comprise fully eighty percent of the collection. An essential portion of this eighty percent is *Pliohippus interpolatus*. Parts of nearly all the skeleton are present, but individual teeth, lower jaws, and palates make up the greater part of the *Pliohippus* remains.

Calippus ansae (Matthew and Stirton)

Plate 3, Fig. 6, 7

This animal is represented by miscellaneous teeth and some few associated molars and premolars. A portion of the left maxillary with complete molar-premolar series demonstrates the characters of the dentition.

Neohipparion eurystyle (Cope)

Plate 4, Figs. 1-4a

There are upper and lower premolars and molars of this horse in the Optima collection. Hesse (1936) noted that in the majority of Pliocene locations on the High Plains members of the *Hipparion* group of horses are the most common type of animal. However, these horses are relatively scarce in the University of Oklahoma collection from Optima.

Nannippus lenticulare (Cope)

Plate 3, Figs. 1-5a

This small equid is represented by a left ramus with only M_3 missing and miscellaneous upper and lower cheek-teeth.

RHINOCEROTIDAE

Teleoceras cf. *fossiger* (Cope)

The principal material consists of a distorted skull with complete dentition, several poorly-preserved palates, five nearly complete lower jaws, numerous

jaw fragments, several hundred assorted molars, premolars, upper incisors and lower incisor tusks, a femur, tibia, radius, astraguli and several metapodials and phalanges.

Camelidae

A large percentage of the camelid material collected at Optima is fragmental. However, among the large number of separate teeth and skeletal fragments have been found many complete bones. Three genera of camels may be distinguished: *Megatylopus*, *Pliauchenia* and *?Alticamelus*. Distinction between individual teeth of these three genera is made very difficult by the large amount of deciduous material. Due to general uniformity in the structure of camelid cheek-teeth, the deciduous teeth of the large *Megatylopus* are hard to distinguish from the adult of *Pliauchenia* unless a complete series is available for study. Although the camelid remains from Optima include several nearly complete mandibles and palates of *Megatylopus*, in none of these specimens is a complete dentition shown. The diagnostic incisors are absent in the more complete dentitions, though rather plentiful as individual teeth. It is chiefly by means of the metapodials that differences are distinguished.

Megatylopus cf. *gigas* Matthew and Cook

Portions of this large and well-advanced tylopod comprise the greater part of the camel remains from Optima. The palate of *M.* cf. *gigas* is distinguished by its large size. The teeth present in the palate are P^3-M^3 on both sides. P^3 and P^4 are one-lobed and greatly reduced. All the molars are two-lobed, with styles making an angle postero-internally. The internal lakes are wide transversely; this distance narrows from M^3 to P^3 respectively. The linear distance from the posterior edge of M^3 to the anterior margin of P^3 is 169 millimeters. The greatest transverse diameter of any cheek-tooth of this palate lies through the anterior lobe of M^2, a distance of 37.2 millimeters on this particular individual.

A mandible in the collection is much more complete than any of the upper dentitions. This specimen shows a complete and well preserved dentition from the canine to M^3 inclusive on each side. The dental formula shown on this jaw is I?, C_1, P_3, M_3. The anterior premolar is compressed and caniniform. Proportions of the jaw are given below:

Measurements in Millimeters	
Length, C_1-M_3 inclusive	271
Length, P_3-M_4 inclusive	174
Length of diastema between P_1 and P_3	41.5
Length of diastema between C_1 and P_1	22.8

The greatest transverse diameter (29.8 millimeters) of any cheek-tooth in this lower jaw is through the posterior lobe of M_2.

From the large series of metapodials of *Megatylopus* in the Optima collection, six complete bones from adult animals were selected for comparative study. The following table shows the proportions of these bones.

Measurements in Millimeters

	Metacarpals				Metatarsal	
	S70	*S64*	*S65*	*S67*	*S5*	*S59*
Total length	524	510	511	501	536	489
Greatest transverse diameter at proximal end	82	80	79.5	79.3	85.4	71.3
Greatest transverse diameter at center of shaft	49.7		48	52.6	51.2	52
Greatest transverse diameter at distal end	102.5	99.2		100.5		90.1
Greatest antero-posterior diameter, proximal end	57.9			55.5		58.3
Greatest antero-posterior diameter, center of shaft	47	46.8	50.8	43.3	53.4	37.8
Greatest antero-posterior diameter, distal end	52	51.4	54.5	53.2	53	44

The metapodials of *Megatylopus* are much larger and stockier than similar bones in the two other genera of Optima camelids. The phalanges of *Megatylopus* are proportional in size and relative shortness to the metapodials. The astraguli are approximately twice the size of the same bones in the smaller camels in every dimension except the antero-posterior length.

Pliauchenia sp. Cope

Remains of this rather medium-sized tylopod are second in abundance in the camel assemblage. The principal specimens referred to this genus are several mandibular fragments, a dozen separate upper and lower cheek-teeth, five metapodials, phalanges and astraguli of intermediate size. A portion of the right ramus shows dentition complete from P_4 to M_3 inclusive. The jaw is much smaller than *Megatylopus* and the teeth are proportionately more compressed. Length from P_4 to M_3 inclusive is 91.7 millimeters; the greatest transverse diameter of the cheek-tooth series is through the posterior lobe of M_2, a distance of 12 millimeters.

The most important material representing *Pliauchenia* in the Optima collection is a set of five metapodials, three metacarpals and two metatarsals. Each bone probably belonged to a different individual although all are adult animals. These metapodials are intermediate in size and weight between the large *Megatylopus* and the slimmer type referred to *Alticamelus*. The following table shows the proportions of these five metapodials.

	Metatarsals	
	S55	*S69*
Total length	338	346
Diameters of proximal end, antero-posterior × transverse	41.6 × 53.8	43.5 × 49.4
Diameters of center of shaft	31 × 33.5	32.1 × 32.4
Diameter of distal end	32.3 × 56.5	31.3 × ?

	Metacarpals		
	S54	*S62*	*S16*
Total length	357	353	342
Diameters of proximal end, antero-posterior × transverse	40 × 54.1	42.8 × 61	41.7 × 53.8
Diameters of center of shaft	32.1 × 34.3	33 × 37.8	30.6 × 35.3
Diameters of distal end	37 × 65.5	37.8 × ?	35.7 × 69.8

?Alticamelus sp.

The presence of this camel in the collection is shown by six metapodials in various stages of preservation. Three first phalanges of slender proportions

have also been referred to this animal. The metapodials are very elongate as compared to *Megatylopus* or *Pliauchenia*. Dimensions of these bones are as follows:

Measurements in Millimeters

	Metatarsals		
	S56	*S58*	*S60*
Total length	?	?	382
Diameters of proximal end, antero-posterior × transverse	39.5 × 43.2	38.5 × 44.1	? × 41.5
Diameters of center of shaft	31 × 26.2	31 × 27	30.5 × 28
Diameters of distal end	? × ?	? × ?	30.1 × 53.3

	Metacarpals		
	S57	*S63*	*S60*
Total length	380	?	429
Diameters of proximal end, antero-posterior × transverse	32.2 × 42.4	38.5 × 44.1	? × 41.5
Diameters of center of shaft	29 × 26.4	31 × 26.5	35.6 × 58.3
Diameters of distal end	? × ?	? × ?	35.6 × 58.3

CERVIDAE

Pediomeryx hemphillensis Stirton

Plate 4, Figs. 5-7a

?Drepanomeryx, Hesse, Univ. Calif. Bull. Geol. Sci., Vol. 24, (1936), p. 64.
Pediomeryx hemphillensis, Stirton, *Jour. Paleont.*, Vol. 10, No. 7, (1936), pp. 644-647.
Yumaceras falkenbachi, Frick, *Bull. Amer. Mus. Nat. Hist.*, Vol. 69, (1937), p. 144.

Several upper and lower cheek-teeth in the Optima collection are identified as *Pediomeryx* through a comparison with figures and a description of this genus by Stirton (1936a). Frick (1937) has proposed the genus *Yumaceras* (Genotype, *Yumaceras figginsi*, from Yuma County, Colorado) and lists a new species, *falkenbachi*, from the Optima fauna. A comparison between *Pediomeryx hemphillensis* and *Yumaceras falkenbachi* leads the writer to conclude that these two should be included under the same genus and species, with only a possible varietal difference separating the two animals. Consequently, *Yumaceras* should be a synonym of *Pediomeryx*.

ANTILOCAPRIDAE

Capromeryx altidens (Matthew)

Plate 4, Figs. 8, 9

Principal material of *C. altidens* consists of two nearly complete rami, several hundred upper and lower molars and premolars, a portion of the pelvis, astraguli, calcanea, first and second phalanges, and a complete metatarsal. Stirton (1938) has demonstrated that the proposed genus and species *Texoceras guymonensis* Frick and *T. minorei* Frick from the Optima fauna are possibly synonymous to *C. altidens*.

TAGASSUIDAE

Prosthennops sp. Gidley

Canine tusks and miscellaneous upper and lower cheek-teeth show the presence of this moderately advanced dicotylid in the Optima fauna. Like practically all the more advanced Tagassuidae, the upper and lower cheek-teeth are exceedingly difficult to distinguish unless they are in a complete series. The canines show similar construction to *Platygonus* (Brown, 1873) and *Mylohyus* (Frick, 1925) but are more compressed than *Mylohyus* and are smaller than *Platygonus*. A left M_3 shows a uniquely simple crown. It is divided into three transverse lophs: the anterior two are bi-cuspate and the posterior one is mono-cuspate. The only accessory cusp is situated immediately posterior to the anterior loph. This tooth approaches *Mylohyus* and *Platygonus* in structure but the cuspate lophs are not so prominent, so high, nor so widely separated as in the two more advanced genera. Other cheek-teeth of the Optima form show more complications through the addition of cuspules. Apparently the Optima animal is much more complex in cusp arrangement than *Prosthennops edensis* Frick (1925) or *P. longirostris* Thorpe (1924), but is not so complex as *P. serus* Cope as figured by Matthew (1918). In many respects *Prosthennops* sp. from Optima is close to *P. xiphodonticus* Barbour (1924), being, however, considerably larger than *xiphodonticus*. *P. niobrarensis* Colbert (1935) also shows similar complexity of structure to the Optima peccary, but this Nebraska specimen is also smaller than the Oklahoma one. In the absence of more complete dentitions or of more complete skeletal material it is thought inexpedient to place the peccary from Optima in any of the described species of *Prosthennops*.

MASTODONTIDAE

Pliomastodon sp. Osborn

The order Proboscidea is represented in the Optima fauna by this short-jawed true mastodon. *Pliomastodon* has been described from the Upper Snake Creek of Nebraska, the Upper (?) Pontian and Levantian of Hungary, the Bone Valley of Florida and the Etchegoin of California. Principal material is an incomplete right and left ramus, upper and lower cheek-teeth, deciduous and permanent upper and lower tusks, one thoracic vertebra and a portion of a femur. Enough of each ramus is present to show that the animal was intermediate between *Miomastodon* and *Mastodon* in the length of the mandible.

A right M_3 in the collection compares favorably with *P. matthewi* Osborn (1936) from Snake Creek in having a rapidly narrowing posterior half of the crown including the third and fourth crests. This tooth measures 195 x 85 millimeters in an antero-posterior x transverse dimension. However a M^3 from Optima differs from the similar tooth in *P. matthewi* by possessing a bi-cusped rudimentary fifth crest rather than a single-cusper fifth crest. This tooth in the Optima mastodon measures 194 x 102 (?) millimeters.

The remainder of the *Pliomastodon* molars, M1 and M2 above and below, are three-crested with traces of trefoils. The second molar above and below shows a rudimentary fourth crest. P_2 (?) has two main crests with a rudimentary third crest.

MEGALONYCHINAE

Gen. et sp. indet.

Plate 2, Figs. 5-6a

An upper and lower caniniform tooth in the University of Oklahoma collection are placed in the above sub-family. The lower caniniform tooth is compressed and shows a meniscoid cross section like *Megalonyx jeffersonii* (Desmarest). The Optima tooth also shows a trace of the characteristic inner bulge of the *jeffersonii* tooth but is much smaller than the Pleistocene form.

RODENTIA

MYLAGAULIDAE

Mylagaulus sp. Cope

Plate 2, Figs. 1, 2

Contained in the Optima collection are three rather large mylagaulid cheek-teeth. Matthew (1924) has pointed out that the genera of Mylagaulidae remain in considerable doubt and confusion. Apparently the teeth differ to such a degree in enamel pattern through wear that it is likely certain genera and species distinguished through variation of these characters are invalid. The size of the three teeth from Optima is equal to that of like teeth in *M. monodon* Cope from the "Republican River" beds of Nebraska or *M. laevis* Matthew from the Pawnee Creek beds of Colorado. Since no further cranial or skeletal portionsof the mylagaulid from Optima have been found, no species designation has been attempted. Among the rodent assemblage are four incisors of equal size and similar construction to *M. laevis;* these incisors probably belong to the same genus and species as the three cheek-teeth.

Dipoides sp. Schlosser

Plate 2, Figs. 3, 3a

The enamel pattern of a M_3 agrees closely with the pattern of *Dipoides stirtoni* Wilson (1934); however, the size of the Optima tooth is slightly greater than *D. stirtoni*. Comparative measurements follow:

Measurements in Millimeters

	D. stirtoni C.I.T. No. 1662 Rome, Oregon	*Dipoides* sp. O.M.P. No. *29-26-S3* Optima
Antero-posterior diameter of M_3	5.1	6.2
Transverse diameter of M_3	4.3	4.5

The antero-internal inflection of the enamel is much more prominent in the Optima tooth than it is in *D. stirtoni*. In addition, *Dipoides* sp. from Optima contains the external and internal inflections of the enamel characteristic of the genus *Dipoides*.

LAGAMORPHA

LEPORIDAE

Hypolagus cf. *vetus* (Kellogg)

Plate 2, Fig. 4

This hare is represented by a portion of a left ramus, with included P_3, and two non-associated incisor teeth. *H.* cf. *vetus* is in close accord with the characters of the genus and species outlined by Kellogg (1910) and Dice

(1917). The Optima animal was a large hare, for it is only slightly smaller than *Lepus californicus*.

Conclusions

In all but a few species the animal assemblage at Optima is identical with that from the Hemphill locality. The abundance of grazing ungulates in the Optima fauna as compared to browsing types indicates that the region was predominantly a broad, open, short-grass country. The scarcity of lagamorphs and rodents in the fauna does not necessarily signify that these animals were rare in the area at that time, but rather that their habits are not such as to lead to their burial in the deposits. It is also possible that many of the smaller bones have been broken up and disseminated. The occurrence of deer, bear, opossum(?), beaver and sloth together with the described fox and lynx indicate that the region was in part a forested country. Alligator remains suggest that the Middle Pliocene climate was warmer and more humid than now and that the Pliocene stream was more sluggish than present-day streams in the area, for alligators frequent quieter and deeper waters.

At Rock Creek on the "Staked Plains" in the Panhandle of Texas, fossiliferous Pleistocene beds have been cut through by the erosion responsible for the large canyons of that region. Pleistocene deposits have been laid down in canyons cut into the Ogallala formation in Cimarron County, Oklahoma. One may conclude from this evidence that the High Plains territory of the Oklahoma and Texas Panhandles was uplifted in Upper Pliocene or Pleistocene time. Texas County in Middle Pliocene time was largely an open or plains country with most of the forested areas confined to the river bottoms and stream valleys.

Faunal Summary at Optima

REPTILIA

TESTUDINIDAE gen. et sp. indet.

CROCODILIDAE gen. et. sp. indet.*

MAMMALIA

DIDELPHIIDAE gen. et sp. indet.*

CANIDAE
- *Osteoborus cyonoides* (Martin)
- *Vulpes stenognathus* Savage n. sp.*

URSIDAE
- *Agriotherium schneideri* Sellards

MUSTELIDAE
- *?Plesiogulo*
- *Taxidea*

FELIDAE
- *Machaerodus catacopis* Cope
- *M. (Heterofelis) coloradensis* (Cook)*
- *Felis proterolyncis* Savage n. sp.*

EQUIDAE
- *Pliohippus interpolatus* (Cope)
- *Calippus ansae* (Matthew and Stirton)
- *Neohipparion eurystyle* (Cope)
- *?Hipparion*
- *Nannippus lenticulare* (Cope)*

RHINOCEROTIDAE
- *Teleoceras* cf. *fossiger* (Cope)

CAMELIDAE
- *Megatylopus* cf. *gigas* (Matthew and Cook)*
- *Pliauchenia* sp. Cope
- *?Alticamelus* sp.*

CERVIDAE
- *Pediomeryx hemphillensis* Stirton*

ANTILOCAPRIDAE
- *Capromeryx altidens* (Matthew)

TAGASSUIDAE
- *Prosthennops* sp. Gidley

MASTODONTIDAE
- *Pliomastodon* sp. Osborn*

MEGALONYCHINAE gen. et. sp. indet.*

MYLAGAULIDAE
- *Mylagaulus* sp. Cope
- *?Dipoides* sp. Schlosser*

LEPORIDAE
- *Hypolagus* cf. *vetus* (Kellogg)*

* Indicates family or genus identified from the Optima fauna for the first time.

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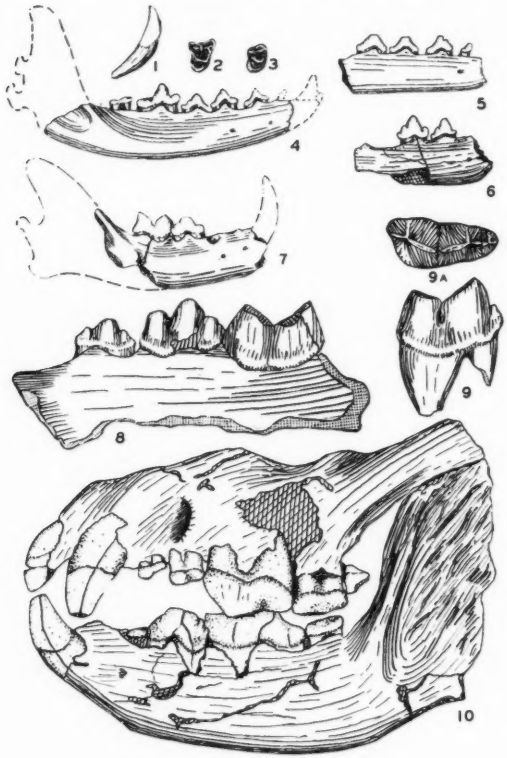

PLATE 1

Figs. 1-5. *Vulpes stenognathus* n. sp.—1. C1, O.M.P. No. *40-25-S10*, dorso-ventral length—25.5 mm. 2. *Paratype*, M1, O.M.P. No. *40-25-S12*, transverse length—11.3 mm. 3. Paratype, M2, O.M.P. No. *40-25-S11*, transverse length—9.2 mm. 4. Cotype, ramus, O.M.P. No. *40-4-S24*, distance from P_2-M_2 inclusive—49 mm. 5. Cotype, ramus, O.M.P. No. *40-4-S10*, distance from P_1-P_4 inclusive—35 mm.

Figs. 6-7. *Felis proterolyncis* n. sp. 6. Cotype, ramus, O.M.P. No. *36-4-S11*, distance from P_3-P_4 inclusive—18.8 mm. 7. Cotype, ramus, O.M.P. No. *36-4-S2*, distance from P_4-M_1 inclusive—22.5 mm.

Fig. 8 *Machaerodus catocopis*, ramus, O.M.P. No. *36-4-S4*, length of molar-premolar series—76.2 mm.

Figs. 9, 9a. *Machaerodus (Heterofelis) coloradensis*, M_1, O.M.P. No. *36-26-S2*, antero-posterior length—32.6 mm.

Fig. 10. *Osteoborus cyonoides*, portion of skull and ramus, O.M.P. No. *40-1-S21*, distance from P2-M1 inclusive—64.6 mm.

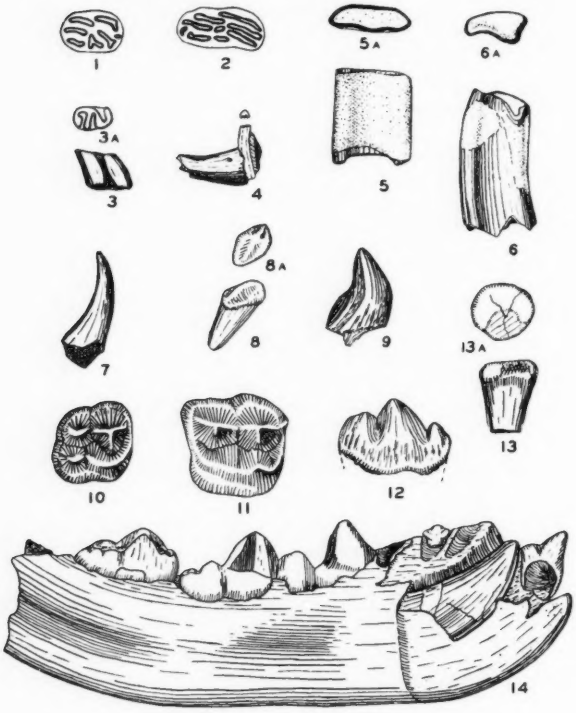

PLATE 2

Figs. 1-2. *Mylagaulus* sp. 1. Cheek-tooth, O.M.P. No. *29-25-S5*, antero-posterior length—9.6 mm. 2. Cheek-tooth, O.M.P. No. *29-26-S2*, antero-posterior length—13.7 mm.

Figs. 3, 3a. *?Dipoides* sp., $M_{?}$, O.M.P. No. *29-26-S3*, antero-posterior length—6.2 mm.

Fig. 4. *Hypolagus* cf. *vetus*, fragment of ramus, O.M.P. No. *29-4-S52*, antero-posterior length of specimen—26.7 mm.

Fig. 5, 5a-6, 6a. Megalonychinae, gen. et sp. indet. 5, 5a. Lower caniniform tooth, O.M.P. No. *41-26-S1*, *antero-posterior* length—24.8 mm. 6, 6a. Upper canniniform tooth, O.M.P. No. *41*-BE-*S2*, antero-posterior length—19 mm.

Fig. 7. Didelphiidae, gen. et sp. indet., C1, O.M.P. No. *12-25-S1*, dorso-ventral length—36 mm.

Figs. 8, 8a-14. *Agriotherium schneideri*. 8, 8a. P_1 (?), O.M.P. No. *33-25c-S2*, antero-posterior length—15.8 mm. 9. I3 (?), O.M.P. No. *33-25a-S1*, dorso-ventral

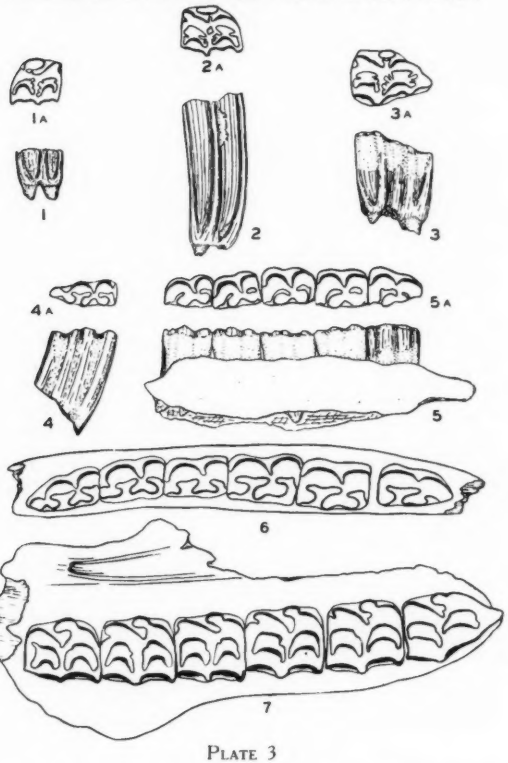

PLATE 3

Figs. 1, 1a-5a. *Nannippus lenticulare*. 1, 1a. Upper cheek-tooth, O.M.P. No. *16-25d-S43*, antero-posterior length—16.2 mm. 2, 2a. Upper cheek-tooth, O.M.P. No. *16-25c-S43*, antero-posterior length—18.6 mm. 3, 3a. Upper cheek-tooth, O.M.P. No. *16-25c-S43*, antero-posterior length—24 mm. 4, 4a. M_3, O.M.P. No. *16-26-S20*, antero-posterior length—21 mm. 5, 5a. Ramus, O.M.P. No. *16-4-S59*, distance from P_2-M_2 inclusive—77.5 mm.

Figs. 6-7. *Calippus ansae*. 6. Ramus, O.M.P. No. *16-4-S58*, length of molar-premolar series—127.3 mm. 7. Upper jaw, O.M.P. No. *16-25-S4*, length of molar-premolar series—143.7 mm.

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length—30.3 mm. 10. M2, O.M.P. No. *33-25d-S7*, antero-posterior length—24.6 mm. 11. M1, O.M.P. No. *33-25d-S1*, antero-posterior length—31.5 mm. 12. P4, O.M.P. No. *33-25c-S1*, antero-posterior length—33.5 mm. 13. M_3, O.M.P. No. *33-26d-S3*, dorso-ventral length—22 mm. 14. Ramus, O.M.P. No. *33-4-S1*, distance from M_1-M_2 inclusive—73.6 mm.

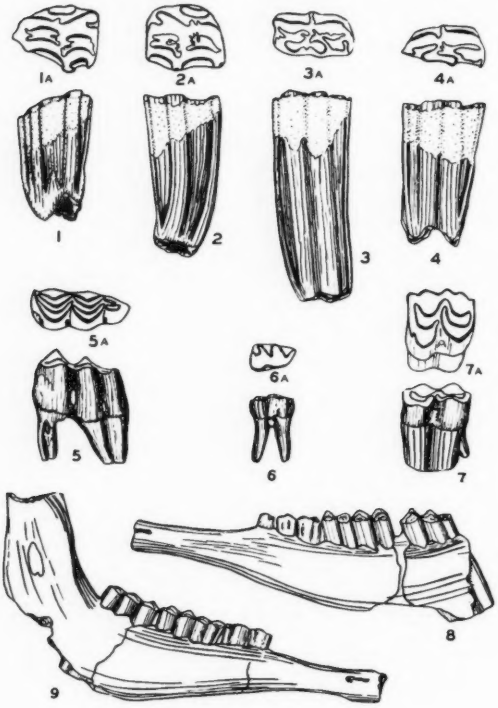


PLATE 4

Figs. 1, 1a-4a. *Neohipparion eurystyle*. 1, 1a. Upper cheek-tooth, O.M.P. No. *16-25-S42*, antero-posterior length—26 mm. 2, 2a. Upper cheek-tooth, O.M.P. No. *16-25c-S42*, antero-posterior length—24.4 mm. 3, 3a. Lower cheek-tooth, O.M.P. No. *16-26-S19*, antero-posterior length—24 mm. 4, 4a. Lower cheek-tooth, O.M.P. No. *16-26c-S19*, antero-posterior length—25 mm.

Figs. 5, 5a-7a. *Pediomeryx hemphillensis*. 5, 5a. M_3, O.M.P. No. *23-26d-S2*, antero-posterior length—13.2 mm. 7, 7a. Upper cheek-tooth, O.M.P. No. *23-25d-S1*, antero-posterior length—20.5 mm.

Figs. 8-9. *Capromeryx altidens*. 8. Ramus, O.M.P. No. *24-4-S9*, distance from P_3-M_3 inclusive—60 mm. 9. Ramus, O.M.P. No. *24-4-S8*, distance from P_3-M_3 inclusive—52 mm.

Book Reviews

BIOLOGICAL SYMPOSIA. Edited by Jaques Cattell. The Jaques Cattell Press, Lancaster, Pa. Vol. 1, 238 pp., 1940, $2.50. Vol. 2, 270 pp., 1941, $2.50. Vol. 3, 370 pp., 1941, $3.50.

Biologia Symposia comprise "A Series of Volumes Devoted to Current Symposia in the Field of Biology" and as such represent a welcome addition to the rather limited number of American reviewing journals. The various symposia included in volumes one and two were sponsored by the American Association for the Advancement of Science and its affiliated societies whereas the last one embodied in volume three was originally organized by the American Physiological Society.

Volume one, with a foreword by Albert F. Blakeslee, contains the three symposia presented at the Richmond meeting to celebrate the one hundredth anniversary of the cell theory. The first of these, "The Cell Theory," is not only concerned with its history but also with its present status. The second symposium on "Mating Types and their Interactions in the Ciliate Infusoria" offers a valuable summary of the recent work in this somewhat neglected field of genetics, whereas the third one deals with the latest findings and views on "Chromosome Structure." Thus these symposia form a natural unit in contrast to the diversity of subjects treated in the second volume.

Four symposia, namely "Speciation," "Defense Mechanisms in Plants and Animals," "Biological Basis of Social Problems," and "Regeneration," are incorporated in volume two which is introduced with a foreword by George A. Baitsell. The symposium on "Speciation" is, fortunately or unfortunately, wholly zoological in outlook, a situation which attests a certain unity but omits possibly valuable viewpoints which might be offered by the botanist. Perhaps "Vertebrate Speciation" would have indicated more adequately its real nature. In the symposium on the "Biological Basis of Social Problems," on the other hand, the boundaries of conventional biology disappear and connections with the "metabiological" aspects of Man are sought.

By comparison, volume three is devoted entirely to one subject, i.e., "Muscle," and the printed version transgresses far beyond the original symposium. Under the editorship of Wallace O. Fenn, new contributions were solicited, discussions incorporated and amended and all other necessary changes made to produce as comprehensive a work as the present world conditions would permit. Although admittedly incomplete, this symposium offers nevertheless much valuable information pertaining to the most significant phases of muscle and muscular activity.

Viewed individually and as a group, the symposia included in these volumes differ considerably in several respects. Those comprising volumes one and two appear essentially in their original form while the last one is apparently the outgrowth of careful editorial planning to overcome the confines imposed on its contributors during the meetings. Perhaps the editors of future volumes will adopt the latter policy to ensure fuller treatment of the selected subjects. Finally, the inclusion of some botanical symposia would certainly be a commendable feature of future *Biological Symposia*.

—THEO. JUST.

THE EVOLUTION OF THE LAND PLANTS (EMBRYOPHYTA). By Douglas Houghton Campbell. Stanford University Press, Stanford University, California, 1940. ix + 731 pp., 351 (352) figs. $6.50.

Although one might rightfully infer from the title of the book that it deals with the factors and causes of *The Evolution of the Land Plants*, it is actually a comprehensive record of the morphology and phylogeny of the groups classified as Embryophyta. To be sure, the available information concerning the evolution of the higher plants is an imposing one. Yet the author does not fail to show its lacunae and the need of future work to clarify many disputed issues. Likewise he anticipates differences of

opinion concerning the conclusions reached by him in the interpretation of the factual material now at our disposal.

Following introductory chapters (pp. 1-55) of a general character but mainly concerned with the Archegoniatae, the treatment of the Bryophyta extends from p. 56 to p. 188, that of the Pteridophyta, inclusive of a chapter on "Heterospory and the Seed Habit," from p. 189 to p. 449, that of the Gymnospermae from p. 450 to p. 537, that of the Angiospermae covers only 155 pages (pp. 538-693). This disproportionate allotment of space may be desirable for some reasons but is certainly unfortunate in view of the absence of modern morphological treatises of the largest and most conspicuous group of land plants. Here would have been an opportunity *par excellence* to compare and evaluate the views favoring a monophyletic or a polyphyletic origin of the Angiosperms, or those regarding the nature of the flower and its members, and even those concerning the plant body itself. Much of the taxonomic, distributional, and miscellaneous information given for various orders could have been sacrificed in favor of a more extensive morphological treatment of the class as a whole. It is here where the greatest confusion remains despite the many excellent contributions made in recent years. And, even if the stamens and carpels should eventually turn out to be organs *sui generis*, such an assertion should be proven rather than made categorically. It might also be more consistent with the emphasis placed on the gametophyte throughout the book to support the monophyletic origin of the Angiosperms since it is not very likely that this generation developed independently in different phyla and attained identical levels in all cases. In view of such discrepancies it is even more regrettable that numerous illustrations were reproduced in a form not in keeping with the otherwise high standards of printing maintained by the Stanford University Press.—THEO. JUST.

BIRD HOUSES, Bath and Feeding Shelters, How to Make and Where to Place Them, by Edmund J. Sawyer. Cranbrook Institute of Science, Bulletin No. 1, Third Edition. December, 1940. Price 20 cents.

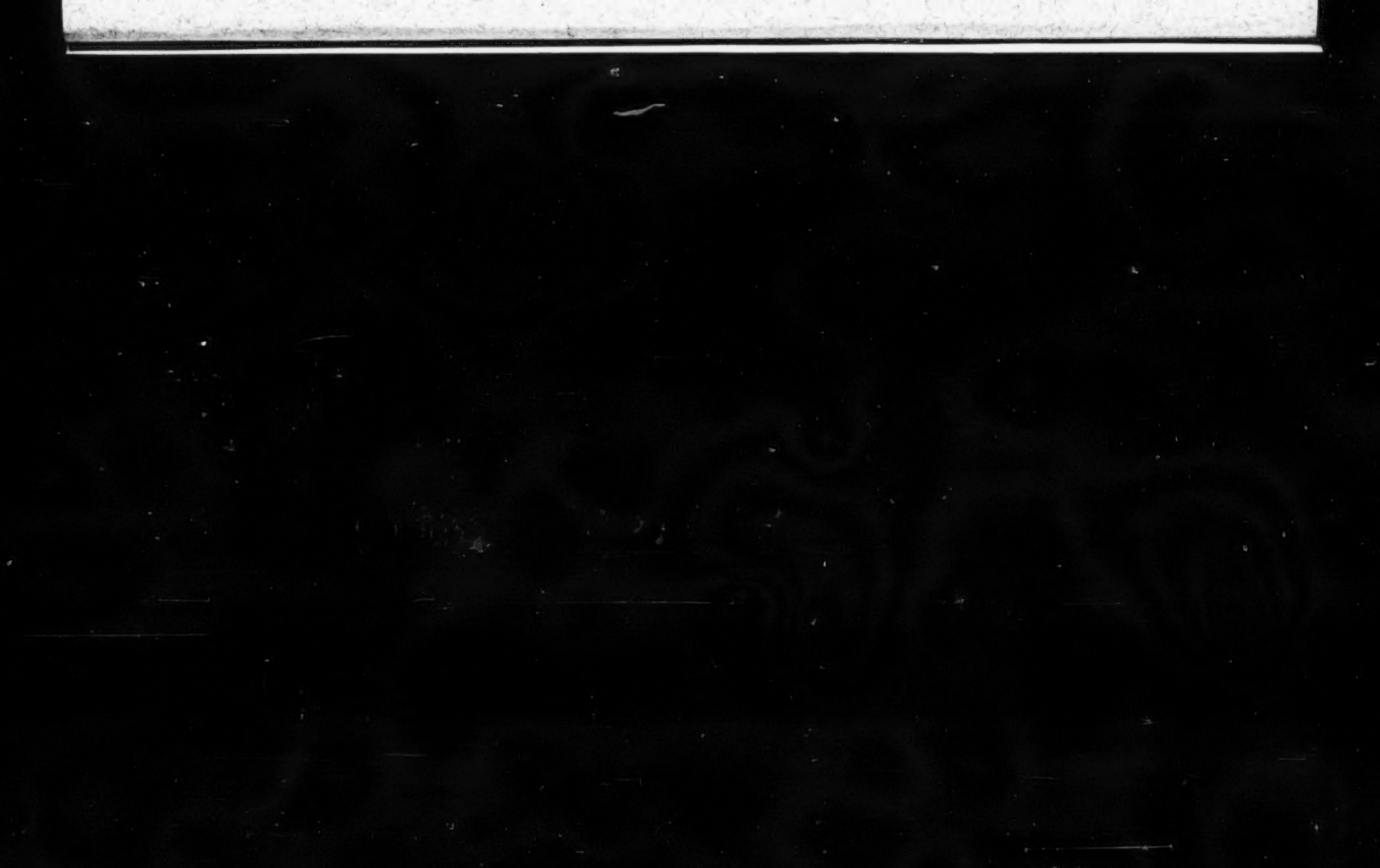
This is an interesting pamphlet which has gone through three editions with a total of 6,500 copies printed. This speaks well for its popularity and probably wide distribution in the Detroit area, or perhaps even the entire Middle West.

It treats of bird houses from the birds' point of view. Too often bird houses are built from the human aspect. It is well illustrated, easy and instructive to read. Complete details as to size and location of house, and size of opening for the bird are given. Perhaps most interesting of all in these days of persecution of predators is the fact that houses are described for the Sparrow Hawk, Saw Whet Owl, Screech Owl and Long-eared Owl.

The author mentions the House Finch that one finds on the streets of Denver, Colorado. This makes the reviewer wonder what would have happened if the English Sparrow and Starling had never been brought to the United States: their places might eventually have been filled by some of our native and much more interesting birds.

All in all Mr. Sawyer has gotten out a very useful and concise bulletin about the ways of attracting birds in the neighborhood of our homes. We hope the third edition will soon be exhausted and many future editions be published.

—MARCUS WARD LYON, JR.



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